



Universidade Federal do Rio Grande
Instituto de Ciências Biológicas
Pós-graduação em Biologia de
Ambientes Aquáticos Continentais



Efeitos da estabilidade hidrológica nas dinâmicas de eclosão de invertebrados aquáticos em áreas úmidas intermitentes

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ATA DE DEFESA DE DISSERTAÇÃO DE MESTRADO EM BIOLOGIA DE AMBIENTES AQUÁTICOS CONTINENTAIS – Nº 002/2026

Às 09:00 hs (nove horas) do dia 19 (dezenove) do mês de fevereiro de 2026 (dois mil e vinte e seis), no Laboratório de Bioinformática do ICB e via Webconferência (<https://conferenciaweb.rnp.br/sala/bioinformatica-icb-furg>), reuniram-se docentes, discentes e comunidade em geral, para a Defesa Pública da Dissertação de Mestrado do acadêmico João Afonso Poester Carvalho. A Dissertação intitulada “**Efeitos da estabilidade hidrológica nas dinâmicas de eclosão de invertebrados aquáticos em áreas úmidas intermitentes**” foi avaliada pela Banca Examinadora composta pela Profa. Dra. Cristina Stenert Maltchik Garcia (Orientadora e Presidente da banca); Prof^ª. Dr^ª. Edélti Faria Albertoni (PPGBAC-FURG) e Prof^ª. Dr^ª. Eneida Maria Eskinazi Sant’Anna (UFOP). Após a defesa e arguição pública, a Banca Examinadora reuniu-se, para deliberação final, e considerou o acadêmico **APROVADO**. Desta forma, o acadêmico concluiu mais uma das etapas necessárias para a obtenção do grau de **MESTRE EM BIOLOGIA DE AMBIENTES AQUÁTICOS CONTINENTAIS**. Nada mais havendo a tratar, às 11h30 (Onze horas e trinta minutos) foi lavrada a presente ata, que lida e aprovada, foi assinada pelos membros da Banca Examinadora, pelo Acadêmico e pela Coordenadora do Curso.

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RESUMO

Invertebrados aquáticos que habitam áreas úmidas intermitentes produzem estágios dormentes que se acumulam no sedimento, formando um banco que pode permanecer viável por muito tempo. O banco de estágios dormentes permite a resiliência da comunidade durante eventos de seca, e permite o recrutamento de indivíduos que eclodem durante o período de inundação. Áreas úmidas intermitentes estão sujeitas a diferentes variações hidrológicas, resultantes, por exemplo, de condições locais de sedimento. A variação hidrológica afeta o ciclo de produção dos ovos e a suas adaptações com relação ao momento de eclosão. Além disso, a eclosão dos organismos após o período de seca, é um momento decisivo para a capacidade de completar o ciclo reprodutivo e se estabelecer na comunidade ativa. O presente trabalho buscou avaliar os efeitos da estabilidade hidrológica de áreas úmidas intermitentes na estrutura da comunidade e na dinâmica de eclosões dos estágios dormentes de invertebrados. Foram selecionadas 10 áreas úmidas em duas matrizes ambientais com estabilidade hidrológica distinta (campos e dunas) e realizado um experimento de incubação de sedimento *ex situ*. O sedimento foi incubado em condições controladas e as eclosões foram monitoradas por 27 dias. Um total de 1469 invertebrados de 22 táxons eclodiram no experimento. A riqueza não foi diferente, entre as campos e dunas nem entre as semanas de hidratação, mas a composição sim. A composição apresentou alta variabilidade e pode ter sido influenciada pela diferença de estabilidade hidrológica. Os resultados demonstram que tanto em áreas úmidas de dunas como de campos, independente da estabilidade hidrológica, os táxons espalham suas eclosões ao longo das semanas de hidratação. A variação de estabilidade hidrológica é um fator a ser considerado nas análises das comunidades de invertebrados de ambientes aquáticos intermitentes, mas, no contexto analisado no presente trabalho, em ambientes com pouca permanência de água, não foi suficiente para resultar em dinâmicas de eclosão com diferenças perceptíveis.

Palavras-chave: dormência; diapausa; quiescência; campos; dunas; Rio Grande do Sul; Pampa; comunidade.

ABSTRACT

Aquatic invertebrates inhabiting intermittent ponds produce dormant stages that accumulate in the sediment, forming a dormant stage bank. The dormant stage bank allows the resilience of the community during drought events, and the recruitment of individuals that hatch during the flooding period. Intermittent ponds are subject to hydrological variations, caused by, for example, local sediment characteristics. Hydrological variation affects the cycle of egg productions and hatching strategies. Furthermore, invertebrate hatching after drought is a decisive moment for the invertebrates to complete their reproductive cycle and establish themselves within the active community. The present study sought to evaluate the effects of hydrological stability in intermittent wetlands on community structure and the hatching dynamics of dormant invertebrate stages. Ten wetlands were selected in two different environmental matrices with distinct hydrological stability (grasslands and dunes) and an *ex situ* hatching experiment was conducted. Sediment was incubated in controlled conditions and hatchlings were monitored for 27 days. A total of 1469 invertebrates from 22 taxa during the experiment. Richness did not vary between grasslands and dunes, nor between the weeks of hydration, but the composition did. The community showed high variability and may have been influenced by differences in hydrological stability. The results demonstrate that in both dune and grassland wetlands, regardless of hydrological stability, taxa spread their hatching throughout the weeks of hydration. Variation in hydrological stability is a key factor to be considered in the analysis of invertebrate communities from intermittent wetlands, but, in the present context, in environments with low water permanence, variation in hydrological stability was insufficient to produce perceptible differences in hatching dynamics

Key-words: dormancy; diapause; quiescence; grasslands; dunes; Rio Grande do Sul; Pampa; community.

APRESENTAÇÃO

O presente trabalho é uma dissertação de mestrado desenvolvida no Programa de Pós-Graduação em Biologia de Ambientes Aquáticos Continentais (PPGBAC). O texto está dividido em: (1) Introdução Geral – detalhando o tema principal da dissertação relacionado à dormência de invertebrados aquáticos e a influência da variação hidrológica na estrutura e dinâmica dessas comunidades; (2) Capítulo 1: “The effects of hydrological stability on the hatching dynamics of aquatic invertebrates in intermittent ponds”, artigo publicado na revista *Wetlands* em 2025”; e (3) Considerações Finais e Perspectivas da dissertação. A Introdução Geral e as Considerações Finais e Perspectivas estão formatadas conforme as normas da ABNT. O Capítulo 1 está formatado conforme as normas do periódico “*Wetlands*”, onde foi publicado.

SUMÁRIO

RESUMO	vi
ABSTRACT	vii
APRESENTAÇÃO.....	viii
LISTA DE FIGURAS	x
LISTA DE TABELAS.....	xi
INTRODUÇÃO GERAL.....	12
Estágios dormentes de invertebrados aquáticos	12
Estrutura do banco de estágios dormentes.....	14
Hidrologia de áreas úmidas intermitentes.....	15
Áreas úmidas intermitentes do extremo sul do Brasil: paisagem e variação hidrológica.....	16
Dinâmica de eclosão do banco de estágios dormentes	17
REFERÊNCIAS	19
CAPÍTULO 1.....	23
ABSTRACT	24
INTRODUCTION	25
MATERIALS AND METHODS	28
Study area	28
Sampling Design and Environmental Variables.....	30
Sediment Sampling, Incubation Experiment and Hatchling Identification	30
Data Analysis.....	32
RESULTS.....	33
Environmental Variables	33
Taxon Richness and Composition	35
DISCUSSION.....	38
ACKNOWLEDGEMENTS.....	43
REFERENCES	43
STATEMENTS AND DECLARATIONS	53
CONSIDERAÇÕES FINAIS E PERSPECTIVAS	59
ANEXOS	61

LISTA DE FIGURAS

CAPÍTULO 1

Figure 1: Map showing the study area, highlighting the selected ponds. The coastal strip is characterized by the dune landscape, which is adjacent to the grassland landscape, toward the continent interior. G = Grassland ponds; D = Dune ponds.

Figure 2: PCA biplot of the environmental variables measured in the ponds, separated by dune and grassland ponds.

Figure 3: Richness of the sampling days in each hydration week, separated by dune and grassland ponds.

Figure 4: Cumulative richness of all ponds, separated by dune and grassland ponds.

Figure 5: a) PCoA plot showing the composition of invertebrate hatchlings and their variation between dune and grassland ponds, and b) among the weeks of the incubation experiment (Weeks 1 to 4).

LISTA DE TABELAS

CAPÍTULO 1

Tabela 1: Mean and standard deviation of the environmental variables obtained for each pond. Pond (G = grassland, D = dune), VC (coefficient of variation of flooding surface area), ORP (oxidation reduction potential), DO (dissolved oxygen) and TDS (total dissolved solids).

Tabela 2: Invertebrate hatchlings and respective sum of individuals per week (W) in both dune and grasslands ponds.

Tabela 3: Summary output of the Indicator Species Analysis for dune and grassland ponds (pond type) and the respective weeks. The analysis allowed combinations of each pond type with the weeks of hydration.

INTRODUÇÃO GERAL

Estágios dormentes de invertebrados aquáticos

Invertebrados aquáticos habitam áreas úmidas intermitentes com diferentes regimes hidrológicos, apresentando adaptações fisiológicas para sobreviver aos ciclos alternados de seca e cheia (Williams, 2006). A dormência é uma forma que muitos invertebrados aquáticos apresentam de sobreviver ao período de dessecação das áreas úmidas temporárias, podendo ser classificada em quiescência e diapausa (Brendonck & De Meester, 2003; Santangelo, 2009; Radzikowski, 2013). A quiescência é uma pausa temporária e reversível no desenvolvimento do organismo, que ocorre em resposta a condições ambientais desfavoráveis (Santangelo, 2009; Radzikowski, 2013). A quiescência pode ocorrer em diferentes estágios ontogenéticos dos organismos, sendo finalizada quando as condições desfavoráveis terminam (Santangelo, 2009; Radzikowski, 2013). Já a diapausa é estágio específico do organismo, que resiste a condições desfavoráveis, mas durante algum tempo é irreversível, muitas vezes necessitando de mudanças fisiológicas e morfológicas (Gyllstrom & Hansson, 2004; Radzikowski, 2013). A diapausa apresenta mecanismos internos de controle, necessitando de sinalizações específicas para finalizar (Santangelo, 2009; Radzikowski, 2013). Esses estágios dormentes são fundamentais para a sobrevivência dos organismos aos períodos de dessecação que ocorrem em áreas úmidas intermitentes, embora também exista produção em ambientes permanentes.

Muitos organismos produzem estágios dormentes que não eclodem imediatamente e se depositam no sedimento (Brendonck & De Meester, 2003). Esse acúmulo de estágios dormentes cria um “banco” no sedimento, que serve como “reservatório” de propágulos após o período de seca (Brendonck & De Meester, 2003). Os estágios dormentes estão distribuídos ao longo de vários estratos do sedimento, mas a camada superior, entre 4 e 6 centímetros de profundidade, constitui o banco ativo, que concentra a maior quantidade de propágulos viáveis (Hoffmann et al., 2023). Em ambientes temporários, o banco de estágios dormentes ativo é a primeira fonte de recrutamento de indivíduos após o retorno da água ao ambiente, juntamente com a dispersão pelo vento e por zoocoria (Lopes et al., 2016).

Táxons de vários grupos de invertebrados aquáticos podem produzir estágios dormentes que compõem o banco (Williams, 2006; Radzikowski, 2013). Espécies

do zooplâncton estão entre as mais utilizadas em trabalhos que avaliam a comunidade dormente, como Copepoda, Cladocera e Rotifera (e.g. Santangelo, 2009; Freiry et al. 2021; Santangelo et al., 2011). Além do zooplâncton, outros grupos de organismos maiores ou de outras classes da biota de áreas úmidas também produzem formas dormentes, como organismos bentônicos e macroinvertebrados (Williams, 2006; Guidetti et al. 2011; Alekseev & Vinogradova, 2019).

Cladóceros são organismos muito representativos da comunidade dormente, cujos ciclos de vida da maioria das espécies apresentam um estágio em diapausa (Brendonck et al., 2017; Santangelo, 2009). Esses organismos apresentam um ciclo de vida, chamado de partenogênese cíclica, que envolve uma fase longa de reprodução assexuada por partenogênese e posterior troca para reprodução sexuada (Decaestecker et al., 2009). Na maior parte do tempo, as populações de cladóceros são compostas de fêmeas partenogenéticas, que reproduzem por ovos diploides não fertilizados (Decaestecker et al., 2009; Santangelo, 2009; Brendonck et al., 2017). Estímulos bióticos e abióticos induzem a produção de fêmeas gametogênicas e machos, iniciando o ciclo de reprodução sexuada, no qual ocorre fertilização e as fêmeas produzem ovos de resistência (Santangelo, 2009; Smirnov, 2017). Os estímulos para o início da reprodução sexuada são variados, mas em geral envolvem condições estressantes, ou sinalizações que precedem essas condições, como variações na temperatura, fotoperíodo, predação ou alta densidade populacional (Decaestecker et al., 2009; Brendonck et al., 2017).

Rotíferos da classe Monogononta também apresentam um ciclo de vida com partenogênese cíclica (Schroder, 2005; Santangelo, 2009). As populações apresentam fêmeas amíticas que se reproduzem por partenogênese, até o momento em que fêmeas míticas começam a ser produzidas em resposta a estímulos ambientais, e com a produção de machos e fêmeas míticas, ocorre fertilização e produção de ovos em diapausa (Schroder, 2005). Estudos ainda têm tentado avançar para entender quais fatores estão ligados ao início da reprodução mítica, como o aumento da densidade populacional (Schroder, 2005).

As três ordens de Copepoda (Harpacticoida, Calanoida e Cyclopoida) apresentam diferentes tipos de dormência e até mesmo mais de um tipo de estratégia e estágio de vida que pode entrar em dormência (Radzikowski, 2013). Espécies de Calanoida são algumas das mais estudadas em relação à produção de

ovos em diapausa (Dahms, 1995), e produzem ovos que eclodem imediatamente, os ovos subcutâneos (Dahms, 1995; Santangelo, 2009) e ovos em diapausa, que apresentam diferenças morfológicas (Couch et al., 2001). Os Calanoida podem trocar a produção de ovos subcutâneos para ovos em diapausa em resposta à estímulos como predação ou seca (de Stasio, 1989; Hairston et al., 2000; Brendonck et al. 2017). Além disso, outras formas de dormência, como estágios quiescentes e de diapausa nas fases de ovos, náuplios e copepoditos, estão presentes em várias espécies de Calanoida, Hapartcoida e Cyclopoida (Dahms, 1995; Dahms & Qian, 2004).

Outros animais, além do zooplâncton, também compõem o banco de estágios dormentes, produzindo diversas estruturas de dormência em diferentes estágios dos ciclos de vida (Williams, 2006; Alekseev & Vinogradova, 2019). Organismos bentônicos, como Anellida e Nematoda, apresentam cistos e anidrobiose como formas de dormência (Williams, 2006). Tardígrados, por exemplo, produzem tanto estágios quiescentes como em diapausa (Guidetti et al., 2011).

Estrutura do banco de estágios dormentes

A composição do banco de estágios dormentes é fundamental para a sucessão da comunidade, pois as espécies presentes no banco poderão ocupar os primeiros estágios da sucessão que ocorre logo após o início do ciclo hidrológico (Lopes et al., 2016). Além disso, os propágulos ali presentes podem ser acumulados ao longo de diferentes gerações, pois uma parcela dos propágulos não eclode em alguns ciclos hidrológicos, criando um arquivo histórico de espécies da comunidade, além de uma reserva genética (Brendonck & De Meester, 2003).

A ecologia de comunidades busca padrões em como as espécies estão distribuídas em comunidades e quais são os mecanismos envolvidos (Vellend, 2016). Diferentes fatores ambientais têm sido investigados como potenciais responsáveis por padrões de riqueza e composição nos bancos de estágios dormentes (Portinho et al., 2017; Freiry et al., 2021). Tanto fatores de escala ampla, como temperatura regional e precipitação, quanto fatores de escala local, como características químicas da água, e ainda fatores como a distância espacial entre sítios, podem ser responsáveis por selecionar quais espécies conseguem colonizar a comunidade dormente de uma área (Freiry et al., 2021). Alguns autores inclusive têm encontrado diferenças entre os fatores que predizem a estrutura da comunidade ativa e da comunidade dormente (Santangelo et al., 2015). Dentre os fatores que

são estudados como potenciais preditores da comunidade dormente de invertebrados aquáticos, o regime hidrológico tem um papel importante, pois é uma variável intrínseca das áreas úmidas intermitentes e tem um papel fundamental no estímulo à produção dos estágios dormentes (Stenert et al., 2017).

Hidrologia de áreas úmidas intermitentes

Áreas úmidas intermitentes são ecossistemas com diferentes tamanhos, formas e tipos de paisagens nas quais estão inseridas, fatores que influenciam como ocorre o ciclo hidrológico da área, ou seja, o tempo que ela passa com uma coluna d'água e o tempo que passa seca (Williams, 2006; Brendonck et al., 2017). Segundo Mitsch & Gosselink (2015) essa característica de não ser nem um ambiente terrestre bem drenado, nem um ecossistema de águas profundas dá o caráter único desses ambientes. Brendonck et al. (2017) revisaram e definiram como o regime hidrológico é uma variável complexa que integra o hidroperíodo e sua variação, frequência e periodicidade, mostrando que o termo serve para descrever um gradiente de permanência de água, desde áreas quase permanentes até áreas efêmeras, com inundações curtas e espaçadas. O hidroperíodo, nessa definição, é a duração da fase de inundação (Hulsmans et al., 2008; Brendonck et al., 2017).

O regime hidrológico está diretamente relacionado com a capacidade das espécies de colonizarem, se reproduzirem e consequentemente manterem suas populações no ambiente, embora, segundo a revisão de Batzer (2013), quando conduziram o estudo, ainda existia pouco consenso sobre como a hidrologia afeta a biota. Batzer (2013) discute que já foram detectadas relações entre a duração do hidroperíodo e a riqueza de espécies, mas com tendências variáveis de acordo com o local, sem capacidade de generalização e nem de predição, e sendo ainda dificultadas quando outras variáveis são incluídas, como predação.

Uma previsão que pode ser feita é de que áreas úmidas com hidroperíodos longos e previsíveis devem permitir a colonização por mais espécies pela eclosão, dispersão e maior disponibilidade de nichos ecológicos (Brendonck et al., 2017). Entretanto, também foi hipotetizado que a estabilidade pode estar relacionada com menor produção de estágios dormentes, por conta de menos estímulos (Golladay et al., 1997; Stenert et al., 2017). Em áreas úmidas com baixa estabilidade hidrológica, ou seja, sujeitas a inundações imprevisíveis e curtas, os estímulos à produção de estágios dormentes podem estar mais presentes (Stenert et al., 2017).

Essas características e a integração de diferentes variáveis torna o hidroperíodo uma junção complexa e difícil de descrever em padrões, muitas vezes instável e imprevisível, como nos ambientes intermitentes e efêmeros (Hulsmans et al., 2008; Brendonck et al., 2017). A previsibilidade do hidroperíodo é outra informação importante, principalmente para os estágios dormentes que se acumulam do sedimento, pois a previsibilidade de uma inundação, bem como a sua duração, após um período de seca, dita a capacidade do estágio dormente de recolonizar a comunidade ativa e completar seu ciclo de vida. Franch-Gras et al. (2017) encontraram resultados em populações de rotíferos que apoiam a hipótese de que a reprodução sexuada – produzindo estágios dormentes – aumenta em ambientes mais imprevisíveis, embora as taxas de eclosões não tenham sido relacionadas com a imprevisibilidade do sistema.

Áreas úmidas intermitentes do extremo sul do Brasil: paisagem e variação hidrológica

As variações hidrológicas em áreas úmidas são resultado de um conjunto de fatores, como regime de precipitação e temperatura regional, condições locais de sedimento e configuração da paisagem (Williams, 2006; Brendonck et al., 2017). As condições de sedimento podem influenciar a retenção da água nas áreas úmidas, por exemplo (Mitsch & Gosselink, 2015). Sedimentos orgânicos podem reter melhor a água (Mitsch & Gosselink, 2015), mantendo a cobertura da área úmida após períodos de precipitação, o que altera, por exemplo, a duração de hidroperíodos.

No extremo sul do Brasil, na Planície Costeira do Rio Grande do Sul, áreas úmidas são abundantes (Waechter, 1985). Essa região apresenta clima subtropical, com precipitações anuais médias de 1300-1600 milímetros (Alvares et al., 2014). A vegetação é característica do bioma Pampa, além de áreas de restinga nas associadas à faixa litorânea (Dinnerstein et al., 2017). As áreas campestres apresentam uma grande quantidade de áreas úmidas, muitas vezes formadas em pequenas depressões em áreas de campos arenosos característicos do bioma Pampa (Pillar et al., 2009). Além disso, as dunas costeiras também apresentam depressões interdunais que acumulam água (Seeliger et al. 1998). Essas duas paisagens estão intimamente associadas e apresentam grandes quantidades de pequenas sistemas aquáticos temporários. Esses sistemas abrigam espécies de invertebrados aquáticos, as quais dependem da produção de estágios dormentes para sobreviver os períodos de dessecação. Entretanto, ambas as paisagens

apresentam características distintas de vegetação, topografia, sedimento, entre outros.

Dinâmica de eclosão do banco de estágios dormentes

As estratégias de eclosão dos estágios dormentes após o período de inundação também são fundamentais para definir a sucessão da comunidade após o período de inundação e como os estágios dormentes respondem aos estímulos que induzem à eclosão (Eskinazi-Sant'Anna & Pace, 2018; Bandeira et al., 2020; Vendramin et al., 2023). Após o período de seca, a recolonização do ambiente aquático ocorre pela contribuição do banco de ovos dormentes e dispersão por diferentes vetores (Lopes et al., 2016). O momento em que um estágio dormiente eclode pode influenciar a sua capacidade de chegar ao estágio adulto e/ou voltar a se reproduzir, definindo o “sucesso” na eclosão (Vanoverbeke & De Meester, 2009; Vanschoenwinkel et al., 2010). Estágios dormentes depositados em um mesmo momento podem, por exemplo, eclodir em diferentes momentos dentro de um mesmo hidroperíodo ou entre hidroperíodos diferentes (Vanoverbeke & De Meester, 2009; Weber et al., 2025). Portanto, diferentes trabalhos avaliaram o padrão temporal da eclosão de invertebrados do banco de estágios dormentes (Eskinazi-Sant'Anna & Pace, 2018; Bandeira et al., 2020; Vendramin et al., 2023). Ainda, esses estudos podem ser feitos tanto pela abordagem *ex situ*, simulando condições de inundação com os estágios dormentes em laboratório, ou ainda *in situ*, monitorando as eclosões diretamente nas áreas úmidas (Pérez-Martinez et al., 2013; Bandeira et al., 2020).

Estratégias de eclosões adiantadas, atrasadas ou espalhadas podem estar relacionadas com evitar competição e evitar inundações “falsas”, curtas demais para completar o ciclo reprodutivo, bem como para garantir recursos (Vanoverbeke & De Meester, 2009; Jocqué et al., 2010; Eskinazi-Sant'Anna & Pace 2018). Vanoverbeke & De Meester (2009) avaliaram os efeitos de inundações com condições de diferentes estações (começo e final da primavera e verão) no sucesso da eclosão e tempo de resposta em estágios dormentes de *Daphnia magna*. Os autores exploraram a eclosão atrasada em curto período e a eclosão atrasada em período intermediário como estratégias dependentes da imprevisibilidade dos hidroperíodos. Já eclosões adiantadas podem estar relacionadas com dominância competitiva no começo do hidroperíodo (Jocque et al., 2010), mas podem resultar em risco de inundações falsas, por exemplo, por conta de dias com variações nas condições de

temperatura e precipitação, que afetam não só a disponibilidade de água, mas também todo o ciclo de sucessão da área úmida (Vanoverbeke & De Meester, 2009).

Eskinazi-Sant'Anna & Pace (2018) também investigaram diferenças no padrão temporal de eclosão entre ambientes permanentes, intermitentes/sazonais e episódicos, encontrando eclosões mais imediatas em ambientes permanentes e eclosões mais atrasadas em ambientes intermitentes/sazonais. Os autores destacaram que algumas espécies atuam como pioneiras nas comunidades de ambientes temporários, além de demonstrarem a influência do regime hidrológico no padrão temporal de eclosões. A eclosão atrasada por alguns dias também é destacada como uma estratégia para garantir que as condições do ambiente após a inundação permitam que o organismo tenha condições favoráveis como recursos disponíveis e tempo para completar o ciclo de vida e reproduzir (Eskinazi-Sant'Anna & Pace, 2018).

Vendramin et al. (2023), encontraram picos de riqueza e abundância de eclosões após a fase intermediária do hidroperíodo em áreas úmidas de uma região de semiárido. Entretanto, outros estudos em localidades distintas encontraram picos de riqueza no começo do hidroperíodo (Hairston et al., 2000; Bandeira et al., 2020), indicando potenciais variações nas estratégias de eclosão em relação às variáveis ambientais e contexto climático.

Essas estratégias de eclosão estão diretamente relacionadas com o contexto hidrológico de uma área úmida (Brendonck et al., 2017; Eskinazi-Sant'Anna & Pace, 2018; Vendramin et al., 2023). O regime hidrológico é caracterizado pela frequência, duração e previsibilidade das inundações (Brendonck et al., 2017). Nesse contexto, estratégias dos organismos para evitar eclosões em inundações curtas, ou para completar o ciclo de vida rapidamente são fundamentais.

Objetivos

Em função das variações hidrológicas terem um efeito potencial na produção e eclosão de estágios dormentes, e, portanto, das comunidades de invertebrados, o presente trabalho busca avaliar como as comunidades de invertebrados dormentes respondem à variação de estabilidade hidrológica entre os ambientes campestres e de dunas. Foram testadas duas hipóteses: (1) que os ambientes de dunas (com menor estabilidade hidrológica) apresentarão maior riqueza de espécies e composição distinta e (2) que os ambientes de dunas apresentarão mais eclosões tardias, enquanto os ambientes de campos apresentarão mais eclosões adiantadas.

REFERÊNCIAS

- ALEKSEEV, V. R.; VINOGRADOVA, E. B. Introduction to Dormancy in Aquatic Invertebrates: Mechanism of Induction and Termination, Hormonal and Molecular-Genetic Basis. In: ALEKSEEV, V.; PINEL-ALLOUL, B. (eds.). **Dormancy in Aquatic Organisms. Theory, Human Use and Modeling**. Springer, 2019.
- ALVARES, C. A.; STAPE, J. L.; SENTELHAS, P. C.; et al. Köppen's climate classification map for Brazil. **Meteorologische Zeitschrift**, v. 22, n. 6, p. 711–728, 2014.
- BANDEIRA, M. G. DA S.; MARTINS, K. P.; PALMA-SILVA, C.; HEPP, L. U.; ALBERTONI, E. F. Hydration time influences microcrustacean hatching in intermittent wetlands: in situ and ex situ approaches. **Hydrobiologia**, v. 847, n. 15, p. 3227–3245, 2020.
- BATZER, D. P. The Seemingly Intractable Ecological Responses of Invertebrates in North American Wetlands: A Review. **Wetlands**, v. 33, n. 1, p. 1–15, 2013.
- BRENDONCK, L.; MEESTER, L. D. Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment. **Hydrobiologia**, v. 491, n. 1–3, p. 65–84, 2003.
- BRENDONCK, L.; PINCEEL, T.; ORTELLS, R. Dormancy and dispersal as mediators of zooplankton population and community dynamics along a hydrological disturbance gradient in inland temporary pools. **Hydrobiologia**, v. 796, p. 201 – 222, 2017.
- COUCH, K. M.; DOWNES, M.; BURNS, C. W. Morphological differences between subitaneous and diapause eggs of *Boeckella triarticulata* (Copepoda: Calanoida). **Freshwater Biology**, v. 46, n. 7, p. 925–933, 2001.
- DAHMS, H. U. **Dormancy in the Copepoda-an overview**, v. 306, p. 199 – 211, 1995.
- DAHMS, H. U.; QIAN, P.-Y. Life histories of the Harpacticoida (Copepoda, Crustacea): a comparison with meiofauna and macrofauna. **Journal of Natural History**, v. 38, n. 14, p. 1725–1734, 2004.
- DECAESTECKER, E.; MEESTER, L. D.; MERGEAY, J. Cyclical Parthenogenesis in *Daphnia*: Sexual Versus Asexual Reproduction. In: SCHON, I.; MARTENS, K.; DIJK, P. (eds.) **Lost Sex: The Evolutionary Biology of Parthenogenesis**. Springer Netherlands, 2009.

DE STASIO, B. T. D. The Seed Bank of a Freshwater Crustacean: Copepodology for the Plant Ecologist. **Ecology**, v. 70, n. 5, p. 1377–1389, 1989.

DINNERSTEIN, E.; OLSON, D.; JOSHI, A.; et al. An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm. **BioScience**, v. 67, n. 6, p. 534–545, 2017.

ESKINAZI-SANT'ANNA, E. M.; PACE, M. L. The potential of the zooplankton resting-stage bank to restore communities in permanent and temporary waterbodies. **Journal of Plankton Research**, v. 40, n. 4, p. 458–470, 2018.

FRANCH-GRAS, L.; GARCÍA-ROGER, E. M.; SERRA, M.; CARMONA, M. J. Adaptation in response to environmental unpredictability. **Proceedings of the Royal Society B: Biological Sciences**, v. 284, n. 1868, 2017.

FREIRY, R. F.; PIRES, M. M.; GOUVEA, A.; et al. Ecological correlates of the alpha and beta diversity of zooplankton hatchling communities in seasonal subtropical ponds. **Ecological Research**, v. 36, n. 3, p. 464–477, 2021.

GOLLADAY, S. W.; TAYLOR, B. W.; PALIK, B. J. Invertebrate communities of forested limesink wetlands in southwest Georgia, USA: Habitat use and influence of extended inundation. **Wetlands**, v. 17, n. 3, p. 383–393, 1997.

GUIDETTI, R.; ALTIERO, T.; REBECCHI, L. On dormancy strategies in tardigrades. **Journal of Insect Physiology**, v. 57, p. 567 – 576, 2011.

GYLLSTRÖM, M.; HANSSON, L. A. Dormancy in freshwater zooplankton: Induction, termination and the importance of benthic-pelagic coupling. **Aquatic Sciences**, v. 66, p. 274 – 295, 2004.

HAIRSTON, N. G.; HANSEN, A.; SCHAFFNER, W. R. The effect of diapause emergence on the seasonal dynamics of a zooplankton assemblage. **Freshwater Biology**, v. 45, n. 2, p. 133–145, 2000.

HOFFMANN, P. H.; ADOLFO, A.; PIU, A. G.; et al. Invertebrate Richness and Hatching Decrease with Sediment Depth in Neotropical Intermittent Ponds. **Wetlands**, v. 43, n. 3, 2023.

HULSMANS, A.; VANSCHOENWINKEL, B.; PYKE, C.; RIDDOCH, B. J.; BRENDONCK, L. Quantifying the Hydroregime of a Temporary Pool Habitat: A Modelling Approach for Ephemeral Rock Pools in SE Botswana. **Ecosystems**, v. 11, n. 1, p. 89–100, 2008.

JOCQUE, M.; VANSCHOENWINKEL, B.; BRENDONCK, L. Anostracan monopolisation of early successional phases in temporary waters? **Fundamental and Applied Limnology**, v. 176, n. 2, p. 127–132, 2010.

LOPES, P. M.; BOZELLI, R.; BINI, L. M.; SANTANGELO, J. M.; DECLERCK, S. A. J. Contributions of airborne dispersal and dormant propagule recruitment to the assembly of rotifer and crustacean zooplankton communities in temporary ponds. **Freshwater Biology**, v. 61, n. 5, p. 658–669, 2016.

MITSCH, W.; GOSSELINK, J. **Wetlands**. 5. ed. John Wiley & Sons, 2015.

PÉREZ-MARTÍNEZ, C.; JIMÉNEZ, L.; MORENO, E.; CONDE-PORCUNA, J. M. Emergence pattern and hatching cues of *Daphnia pulicaria* (Crustacea, Cladocera) in an alpine lake. **Hydrobiologia**, v. 707, n. 1, p. 47–57, 2013.

PILLAR, V. P.; MÜLLER, S. C.; CASTILHOS, Z. M. S.; JACQUES, A. V. A. (eds.). **Campos Sulinos: Conservação e Uso Sustentável da Biodiversidade**. Brasília: MMA, 2009

PORTINHO, J. L.; NIELSEN, D. L.; NING, N.; PAUL, W.; NOGUEIRA, M. Spatial variability of aquatic plant and microfaunal seed and egg bank communities within a forested floodplain system of a temperate Australian river. **Aquatic Sciences**, v. 79, n. 3, p. 515–527, 2017.

RADZIKOWSKI, J. Resistance of dormant stages of planktonic invertebrates to adverse environmental conditions. **Journal of Plankton Research**, v. 35, n. 4, p. 707 – 723, 2013.

SANTANGELO, J. M. Produção, Eclosão e Implicações Ecológicas e Evolutivas dos Estágios Dormentes do Zooplâncton. **Limnotemas**, p. 03–35, 2009.

SANTANGELO, J. M.; ESTEVES, F. DE A.; MANCA, M.; BOZELLI, R. L. Abundance, composition and spatial variation in the egg bank of a tropical zooplankton community. **Studies on Neotropical Fauna and Environment**, v. 46, n. 3, p. 225–232, 2011.

SANTANGELO, J. M.; LOPES, P. M.; NASCIMENTO, M. O.; et al. Community structure of resting egg banks and concordance patterns between dormant and active zooplankters in tropical lakes. **Hydrobiologia**, v. 758, n. 1, p. 183–195, 2015.

SCHRÖDER, T. Diapause in Monogonont Rotifers. **Hydrobiologia**, v. 546, n. 1, p. 291–306, 2005.

SEELIGER, U. O Sistema das Dunas Costeiras Frontais. In: SEELIGER, U; ODEBRECHT, C.; CASTELLO, J.P. (Eds.) **Os Ecossistemas Costeiro e Marinho do Extremo Sul do Brasil**. Rio Grande: Editora Ecoscientia, 1998

SMIRNOV, N. **Physiology of the Cladocera**. 2nd ed. Academic Press, 2017.

- STENERT, C.; WÜSTH, R.; PIRES, M. M.; et al. Composition of cladoceran dormant stages in intermittent ponds with different hydroperiod lengths. **Ecological Research**, v. 32, n. 6, p. 921–930, 2017.
- VANOVERBEKE, J.; MEESTER, L. D. Within season short-term hatching delays suggest risk-spreading behaviour in populations of the freshwater cladoceran daphnia. **Ecoscience**, v. 16, n. 4, p. 441–451, 2009.
- VANSCHOENWINKEL, B.; SEAMAN, M.; BRENDONCK, L. Hatching phenology, life history and egg bank size of fairy shrimp Branchiopodopsis spp. (Branchiopoda, Crustacea) in relation to the ephemerality of their rock pool habitat. **Aquatic Ecology**, v. 44, n. 4, p. 771–780, 2010.
- VELLEND, M. **The Theory of Ecological Communities**. Princeton University Press, 2016.
- VENDRAMIN, D.; PIRES, M. M.; MEDEIROS, E. S. F.; STENERT, C.; MALTCHIK, L. Life finds a way: Hatching dynamics of zooplankton dormant stages in intermittent wetlands from the Brazilian tropical semiarid. **Journal of Arid Environments**, v. 212, 2023.
- WAECHTER, J. L. Aspectos ecológicos da vegetação de restinga no Rio Grande do Sul, Brasil. **Comunicações do Museu de Ciências da PUCRS, Série Botânica**, v. 33, p. 49-68, 1985.
- WEBER, V.; ALONSO, F.; GODOY, R. S.; et al. Evolved bet-hedging through maternal effects: developmental trajectory variation in annual killifish across a wet–dry cycle. **Hydrobiologia**, 2025.
- WILLIAMS, D. D. **The Biology of Temporary Waters**. Oxford University Press, 2006.

CAPÍTULO 1

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The effects of hydrological stability on the hatching dynamics of aquatic invertebrates in intermittent ponds

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Abstract

Aquatic invertebrates including zooplanktonic and non-zooplanktonic taxa produce resting stages to persist during drought periods in temporary wetlands. These resting stages provide both resistance for these organisms during drought periods, as well as resilience with the arrival of the first floods. The hydrological stability of temporary wetlands influences the hatching pattern of dormant stages in the invertebrate community. Here, we compare the structure and hatching dynamics of dormant stages of the aquatic invertebrate community of temporary ponds with different levels of hydrological stability. A total of ten temporary ponds were selected - five dune ponds and five grassland ponds. A total of 1,469 invertebrates distributed among 22 taxa emerged from dune and grassland sediments. The total richness of hatchlings did not change between dune and grassland sediments and nor during the weeks of hydration. The differences in habitat characteristics and hydrological stability between dune and grassland ponds may have contributed to the variation in the composition of hatched invertebrates. Furthermore, our results showed that the hatching of dormant stages of the invertebrate community from temporary wetlands is spread throughout the entire surface water period, regardless of pond hydrological stability.

Keywords: dormancy, dune slack, Pampa, temporary wetlands, zooplankton

Introduction

Many species of aquatic invertebrates inhabiting temporary wetlands possess physiological and behavioral adaptations to survive two hydrological extreme periods: flooding and drought (Williams 2006). Dormancy is a strategy adopted by these species to persist during drought periods, involving two key mechanisms: quiescence and diapause (Brendonck and De Meester 2003; Brendonck et al. 2017). Quiescence occurs when the organism enters a hibernation state encased in a protective secretion to endure unfavorable environmental conditions and it can be observed in some species of rotifers and copepods. Diapause occurs when the organism produces resting eggs (via sexual reproduction) that hatch during favorable periods and it can be observed in species of Cladocera, Rotifera, Copepoda and Anostraca, among other aquatic invertebrates (Hairston 1996; Cáceres 1997; Schroder 2005; Santangelo 2009; Radzikowski 2013). For example, non-zooplanktonic aquatic invertebrates have different physiological and behavioral mechanisms to survive desiccation, such as dormant eggs or cysts observed in flatworms, oligochaetes, collembolans, mayflies, beetles, caddisflies and mosquitoes (Williams 2006). Besides, nematodes and tardigrades can also have a dormant stage in life cycle capable of surviving unpredictable habitats (Rebecchi et al. 2007; Guidetti et al. 2011; Vendramin et al. 2022).

Aquatic invertebrates produce resting stages that accumulate in the sediment, forming a dormant bank with strong generation overlap that can remain viable for many years (Hairston and Cáceres 1996; Brendonck and De Meester 2003; Brock et al. 2003). In this sense, the dormant bank acts as a genetic reservoir with important ecological and evolutionary implications, contributing to the resilience of populations and communities during the onset of the first floods (Panarelli et al. 2008; Lopes et al. 2016; Brendonck et al. 2017). The production of dormant stages occurs in response to different environmental

and biotic stimuli, such as variations in temperature, photoperiod, hydroperiod, population density and predation (Nielsen et al. 2000; Batzer and Boix 2016; Vargas et al. 2019; Pires et al. 2023). After rehydration, similar environmental cues can trigger the hatching of dormant stages in invertebrates from temporary wetlands (Araújo et al. 2013; Stenert et al. 2017; Bandeira et al. 2020; Eskinazi-Sant'anna and Pace, 2018; Freiry et al. 2021; Brazil et al. 2022; Vargas et al. 2024).

The alternation between flooding and drying phases in temporary wetlands is a key predictor of the structure and dynamics of dormant stages (Garcia-Roger, 2000; Brendonck and De Meester, 2003; Stenert et al. 2017, Vargas et al. 2019). However, the hydrological regime of temporary wetlands varies in terms of timing, duration, and frequency of floods due to factors such as regional climate, area size, soil characteristics, aquatic vegetation, and connectivity with other aquatic ecosystems (Williams 2006; Mitsch and Gosselink 2015; Vargas et al. 2024). Sediment texture and composition strongly influence the hydrological regime; sandy sediments with low organic matter content reduce the retention and persistence of surface water in temporary wetlands (Penatti and Almeida 2012; Mitsch and Gosselink 2015). In this context, the variable gradient of water level fluctuations strongly influences the production, hatching, and reproductive success of populations with dormant stages in temporary wetlands (Tuytens 2014; Brendonck et al. 2017; Pires et al. 2023; Vargas et al. 2024).

The effects of water level fluctuations (here called hydrological stability) on the structure and hatching dynamics of invertebrate dormant banks may be mediated by environmental cues, such as physical and chemical water variables, which can signal whether a flood will be short or prolonged (Brendonck et al. 1998, 2017). In hydrologically stable wetlands, prolonged and predictable flooding periods are expected to enhance richness over time through hatching from the dormant bank and dispersal

(Lopes et al. 2016), as well as through the progressive availability of ecological niches (Brendonck et al. 2017). In contrast, more unstable environments, characterized by strong surface water fluctuations and recurrent drying events, are likely to promote more frequent cues for the production and hatching of invertebrate dormant stages (Araújo et al. 2013; Nielsen et al. 2013; Stenert et al. 2017; Tarazona et al. 2017; Brazil et al. 2022; Vargas et al. 2024). However, prolonged drought events, ranging from one year (Vargas et al. 2024) to 30 years (Nielsen et al. 2013), can negatively affect the viability and hatching of invertebrate dormant stages in temporary wetlands. Nonetheless, the effects of hydrological stability on production, hatching and viability of dormant stages are expected to differ among invertebrate taxa, especially in relation to life cycle duration, reproductive strategies, and sensitivity to local environmental factors that vary along the hydroperiod gradient (Brendonck et al. 2017). For example, rotifers may withstand longer drought periods than microcrustaceans in tropical lakes (Portinho and Perbiche-Neves 2025).

The phenology of zooplankton hatching can vary according to the hydrological stability of the system, manifesting as either delayed or early responses (Bandeira et al. 2020; Vendramin et al. 2023). The timing of hatching after flooding is crucial for dormant communities, as it determines their ability to complete their life cycle (Vanoverbeke and De Meester, 2009). Delayed hatching has often been observed in dormant stages of zooplanktonic organisms (Evans and Dennehy, 2005; Martínez-Ruiz and García-Roger, 2015) and is associated with environments hydrologically less stable (Vanoverbeke and De Meester 2009; Brendonck et al. 2017; Vendramin et al. 2022). Moreover, in unstable hydrologically habitats, dormant stages of zooplankton may hatch in small fractions, thus reducing the risk of exhausting the dormant bank in response to short flooding events (Brendonck et al. 2017; Garcia-Roger et al. 2017; Pinceel et al. 2021; Pires et al. 2023).

Non-zooplanktonic invertebrates might also vary the hatching time, such as tardigrades (Guidetti et al. 2011).

In southern Brazil, the relationship between invertebrate dormant communities and the hydrological stability of temporary ponds has not been specifically investigated. In this sense, the aim of this study was to compare the structure and temporal dynamics (phenology) of hatching from dormant stages of aquatic invertebrates among temporary ponds with different levels of hydrological stability. To achieve this, dune and grassland ponds were analyzed in the same geographic and climatic region in southernmost Brazil. Using an ex-situ approach, we compared the richness and composition of hatchlings from dormant communities over four weeks of incubation. Since dune and grassland ponds have distinct sediment compositions that influence water retention capacity and consequently the hydrological stability, which may act as an environmental filter for invertebrate taxa, our first hypothesis is that the richness of hatchlings will be greater in ponds with lower hydrological stability (dunes) than ponds with higher hydrological stability (grasslands), and the composition of hatched invertebrates will differ between dune and grassland ponds. Since delayed hatching has often been associated with hydrologically less stable environments, our second hypothesis is that hatching patterns will be different between ponds with different degrees of hydrological stability; more specifically, more delayed hatching responses are expected to occur equally across all invertebrate taxa in ponds with a lower hydrological stability over time (dunes) than ponds with higher hydrological stability (grasslands).

Material and Methods

Study Area

Sampling was conducted in the Coastal Plain of the Pampa region, in the southernmost portion of Brazil, Rio Grande municipality, Rio Grande do Sul State (Fig. 1). The region has a flat topography and moist subtropical climate. The absence of hills and the low altitude make the precipitation and temperature similar throughout the study area (Rambo 2000). This region presents a sand dune landscape with typical dune herbaceous vegetation, which is replaced by grassland landscape towards the inland continent (Seeliger 1998). Both dune and grassland landscapes are marked by small ponds formed by precipitation, with variable surface flooding area throughout the year, including ponds that dried out from spring to late summer (Seeliger 1998; Pillar et al. 2009). The annual precipitation ranges from 1,300 to 1,600 mm, uniformly distributed throughout the year, without a dry season (Alvares et al. 2013). The mean temperatures range between 14.6 °C in winter and 22.2 °C in summer, and the mean annual temperature is 17.5 °C (Alvares et al. 2013).

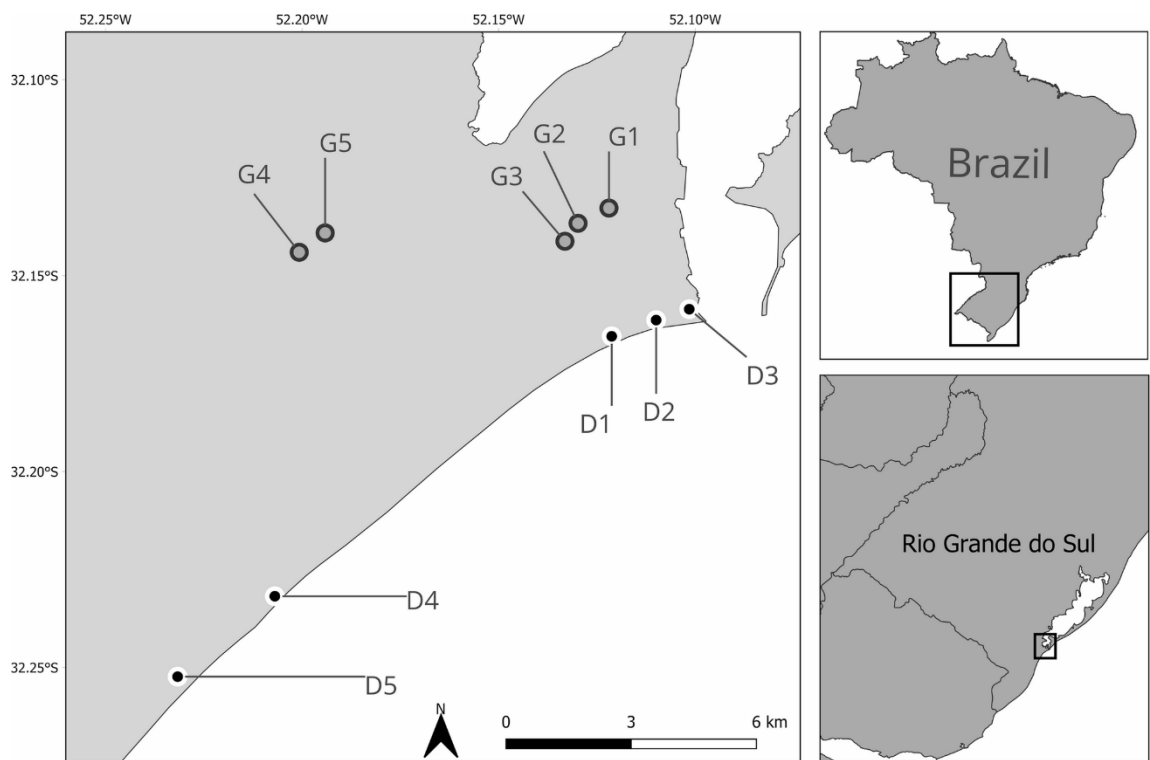


Fig. 1. Map showing the study area, highlighting the selected ponds. The coastal strip is characterized by the dune landscape, which is adjacent to the grassland landscape, toward the continent interior. G = Grassland ponds; D = Dune ponds.

Sampling design and environmental variables

Ten small ponds were selected among many others for the study during March 2024, five ponds in a dune landscape (henceforth ‘dune ponds’) and five ponds in a grassland landscape (henceforth ‘grassland ponds’) (Fig. 1). The selected ponds were isolated (had no connectivity between them), and the minimum distance between them was 700 m. All ponds had similar areas (< 0.2 ha) and water depth < 0.4 m. The following environmental variables were monitored at each pond during a period of nine months, from June 2024 to February 2025 (six times, in June, July, September, November, December, February) to provide a broader description and comparison of the variables between dune and grassland ponds: area (measured by walking around the perimeter of the wetland with a GPS), hydrological stability (measured by the variation of the surface flooding area over the monitoring period) and number of drought events in the monitored months; and water depth, pH, temperature, dissolved oxygen, electrical conductivity, water turbidity, total dissolved solids (TDS), oxidation reduction potential (ORP) and salinity, measured with a multiparameter water quality checker (HORIBA 207 U-22 Water Quality Checker). One sediment sample was collected in each pond for measurement of organic matter percentage in March 2024. The organic matter content was determined by drying the sediment at 60°C for 24 h and burning it for 5 h in an oven at 550°C .

Sediment sampling, incubation experiment and hatchling identification

In each pond, twelve sediment subsamples were randomly collected with a garden trowel (~100 g per subsample) from the topsoil layers (5-cm deep) in March 2024. The subsamples were pooled into a single sample per pond (~1 kg) in 5-L dark plastic bags. All grassland ponds and one dune pond contained water at the time of sediment sampling. In the laboratory, sediments from these ponds were dehydrated in a dark oven at 40 °C for at least 96 hours to standardize desiccation, and subsequently homogenized.

The incubation experiment was conducted in May 2024, using 500 g of the homogenized sediment from each pond. Sediment was distributed into plastic trays (34x18x10 cm), each tray representing one pond. Distilled water was used to submerge the sediment, with a 2 cm water column (Hoffmann et al. 2023), which was maintained constant throughout the incubation by periodically adding distilled water. The experiment lasted 27 days (April 30th to May 27th) and the trays were kept at a temperature of 18 ± 3 °C (comparable with flooded field conditions recorded during the sampling season) and a photoperiod cycle of 12h light/dark, using a climate-controlled room. Hatchlings were collected every 3 to 4 days, specifically on Mondays and Thursdays, using three standardized sweeps with a small hand-net (50 µm mesh size) adapted to the dimensions of the tray. This sampling procedure was used to minimize the chance of parthenogenetic reproduction (Brock et al. 2003; Daré et al. 2024). Hatchlings were isolated and counted under a stereomicroscope and transferred to microtubes with 80% ethanol. Unhatched dormant stages found were returned to the trays exactly as observed. Crustaceans and rotifers were identified to genus or species level when possible, using both specialized literature (Koste 1978; Elmoor-Loureiro 1997; Elmoor-Loureiro 2000; Sousa and Elmoor-Loureiro 2019), consulting specialists and with the assistance of a specialized website for the identification of cladocerans (<https://cladocera.wordpress.com/>).

Data analysis

The hydrological stability of each pond was represented by the coefficient of variation (standard deviation divided by the mean) based on the variation of the surface flooding area over the monitoring period. The environmental variables of dune and grassland ponds were reduced by principal component analysis (PCA) based on the mean values of the water physical and chemical variables measured during the monitoring period and on a single value of the organic matter (since one sediment sample was collected from each pond) and coefficient of variation of flooding surface area. We conducted the PCA to visualize the most important environmental variables (limnological, sediment, and hydrological characteristics) that explain the differences between dune and grassland ponds. Additionally, differences in environmental variables between dune and grassland ponds were analyzed using a multivariate analysis of variance (MANOVA) based on the scores of the first two principal components (Axis 1 and Axis 2) from the PCA ordination.

We built a species accumulation curve to show the increase of the number of taxa for both dune and grassland ponds during the experiment. To compare the richness of hatchlings between dune and grassland ponds (Hypothesis 1) and the temporal hatching patterns among incubation weeks (Hypothesis 2), we used a Generalized Linear Mixed Model (GLMM). We categorized each sampling day for the corresponding week of the experiment (sampling days 1, 2 and 3 = week 1; sampling days 4 and 5 = week 2; sampling days 6 and 7 = week 3; and sampling days 8 and 9 = week 4). In the model, the richness is the response variable, while the hydration week and the pond type (dune and grassland) are the explanatory fixed effects, as well as an interaction effect. Each sampling day was accounted for as a random effect. We fitted the GLMM with Poisson distribution and log link and checked the assumptions of the model with diagnostic plots. We evaluated the significance of model terms using a Likelihood Ratio Test (LRT).

To assess variation in the taxa composition between dune and grassland ponds (Hypothesis 1) and among incubation weeks (Hypothesis 2), we used principal coordinate analysis (PCoA) and permutational multivariate analysis of variance (PERMANOVA) using the Jaccard distance matrix and 9,999 permutations to validate the model significance. We verified the dispersion of beta diversity between weeks, pond types (dune and grassland) and the combinations of both (weeks and pond types), using the betadisper method from vegan package (Oksanen et al. 2024).

The Indicator Species Analysis (IndVal; Dufrêne and Legendre 1997) was utilized to identify invertebrate taxa associated with each pond type and weeks of the incubation experiment. The statistical significance of the observed IV for each invertebrate taxa was assessed through 9,999 permutations. All analytical procedures were performed using the packages vegan (Oksanen et al. 2024), lme4 (Bates 2015), DHAMRA (Hartig 2024), FactoMineR (Lê et al. 2008), ggplot2 (Wickham 2016) and indicpecies (De Cáceres and Legendre 2009) in R v 4.4.0 (R Core Team 2024).

Results

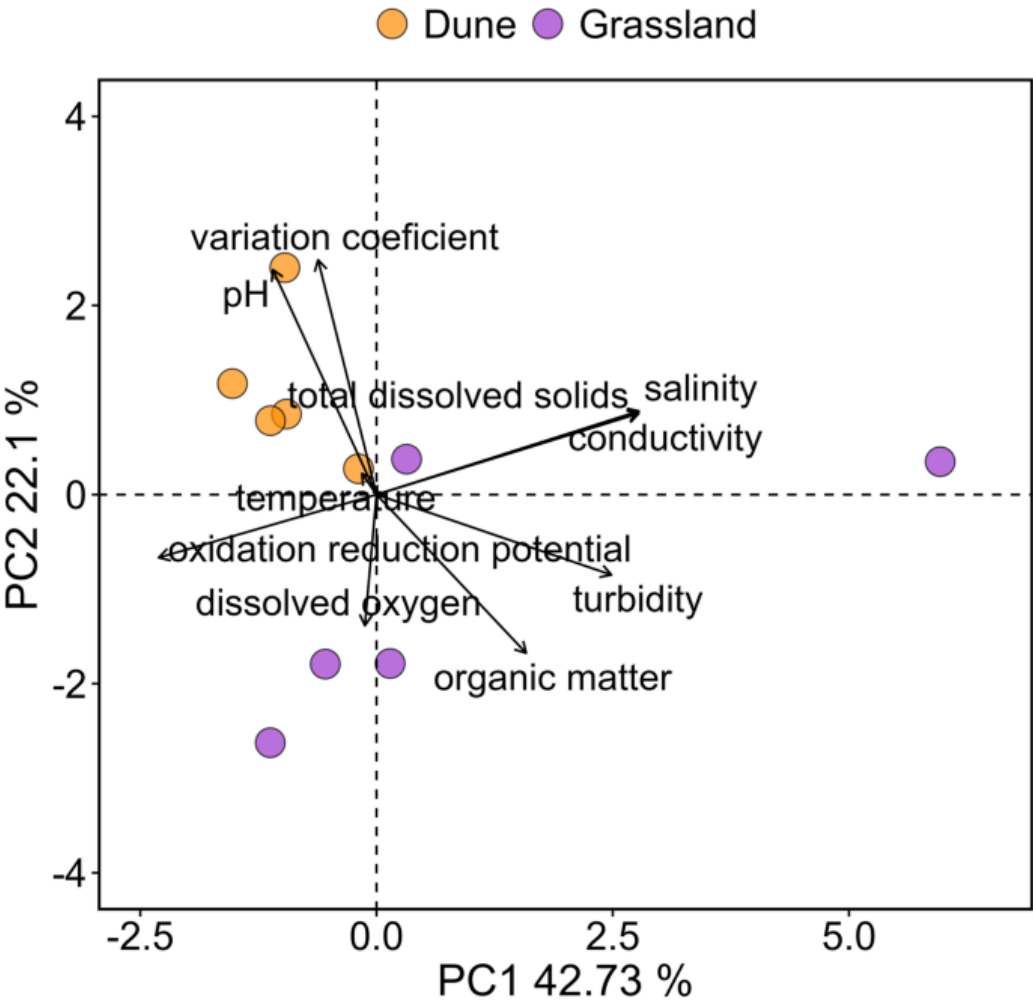
Environmental variables

The PCA showed a separation between grassland and dune ponds based on environmental variables, which was further supported by the results of the multivariate analysis of variance (MANOVA) ($F_{1,8} = 10.837$, $P = 0.007$) (Fig. 2). The two principal components explained 42.73% and 22.1% of the data variation, respectively. The first component was positively correlated with conductivity, turbidity, total dissolved solids, salinity and organic matter percentage and negatively correlated with oxidation reduction potential. The second component was positively correlated with pH and coefficient of variation. Among the environmental variables, pH, temperature and oxidation reduction

potential were higher in dune ponds, whereas turbidity, conductivity and sediment organic matter were higher in grassland ponds (Table 1, Fig. 2). The sediment organic matter ranged from 0.2% to 7.2% in dune ponds, and from 8.4% to 41.7% in grassland ponds (Table 1). The hydrological stability was lower in dune ponds compared to grassland ponds since the average of the coefficient of variation was 102.9% in grassland ponds and 150% in dune ponds. Besides, the grassland ponds had a lower mean number of droughts (1.8) than dune ponds (2.4) during the monitored period (Table 1).

Fig. 2. PCA biplot of the environmental variables measured in the ponds, separated by dune and grassland ponds

Taxon richness and composition



A total of 1,469 invertebrates distributed among 22 taxa emerged from dune and grassland sediments, including zooplanktonic species of crustaceans (cladocerans, anostracans, conchostracans, ostracods and copepods), bdelloid and monogonont rotifers, and non-zooplanktonic invertebrate taxa such as collembolans, Acari, nematodes, oligochaetes, microturbellarians and tardigrades (Table 2). Eight taxa were found in both dune and grassland ponds. However, some taxa emerged exclusively from dune sediments (seven taxa), such as collembolans, the monogonont rotifers *Dipleuchlanis propatula* and *Euchlanis* sp., the harpacticoid copepods and the cladocerans *Pleuroxus* sp., *Ovalona glabra* and *Ceriodaphnia quadrangula*. Some invertebrate taxa occurred only in sediments rehydrated from grassland ponds (seven taxa), including monogonont and bdelloid rotifers, anostracans, conchostracans and the cladocerans *Simocephalus* cf. *serrulatus* and *Leydigia striata*.

The total richness of hatchlings did not change between dune and grassland sediments (GLMM, $LR\ Chisq = 0.152$, $d.f. = 1$, $P = 0.697$) nor during the weeks of hydration (GLMM, $LR\ Chisq = 3.272$, $d.f. = 2$, $P = 0.195$) (Fig. 3). No interaction between weeks and pond types was observed in invertebrate richness (GLMM, $LR\ Chisq = 4.022$, $d.f. = 3$, $P = 0.259$) (Fig. 3). The species accumulation curve showed that the increase of invertebrate taxa richness was similar and gradual between dune and grassland sediments during the sampling events of the experiment (Fig. 4).

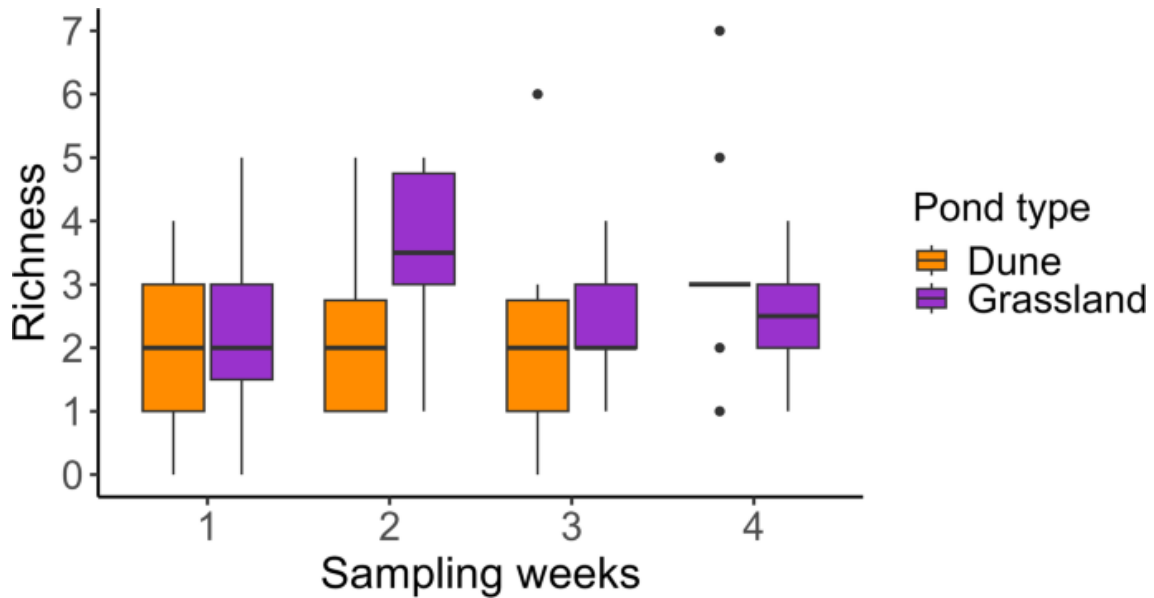


Fig. 3. Richness of the sampling days in each hydration week, separated by dune and grassland ponds.

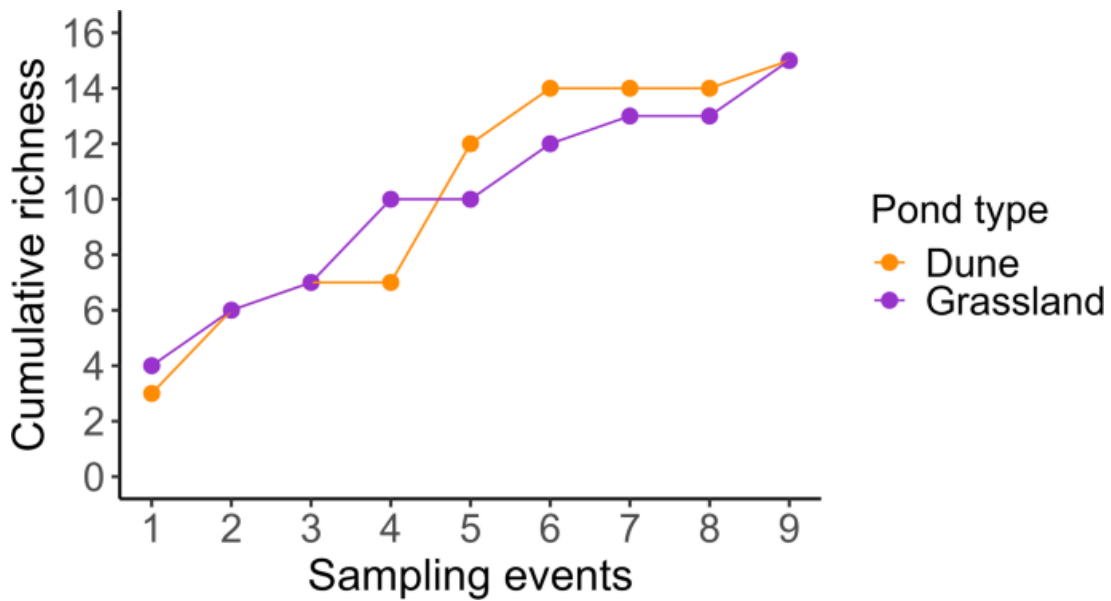


Fig. 4. Cumulative richness of all ponds, separated by dune and grassland ponds.

The composition of invertebrate hatchlings varied between grassland and dune ponds ($R^2 = 0.036$, $F_{1,79} = 3.693$, $P = 0.001$), and among the weeks of the incubation experiment ($R^2 = 0.124$, $F_{3,79} = 4.174$, $P = 0.001$) (Fig. 5). There was an interaction between weeks and pond types ($R^2 = 0.053$, $F_{3,79} = 1.806$, $P = 0.025$), showing that the composition changed between grassland and dune ponds over the experiment. The

composition variation between dune and grassland ponds was more affected by internal dispersion of beta diversity, as shown by the Betadisper analysis ($F_{1,85} = 7.981$, $P = 0.014$, Fig. 5a). Similarly, the composition variation among weeks was also affected by internal dispersion in both dune and grassland ponds ($F_{3,83} = 3.890$, $P = 0.010$. Fig. 5b). Dune ponds showed greater visual segregation than grassland ponds in the composition of invertebrate hatchlings between the initial (early hatching) and final weeks (delayed hatching) of the experiment, which may be related to the interaction effect observed in the PERMANOVA (Fig. 5b).

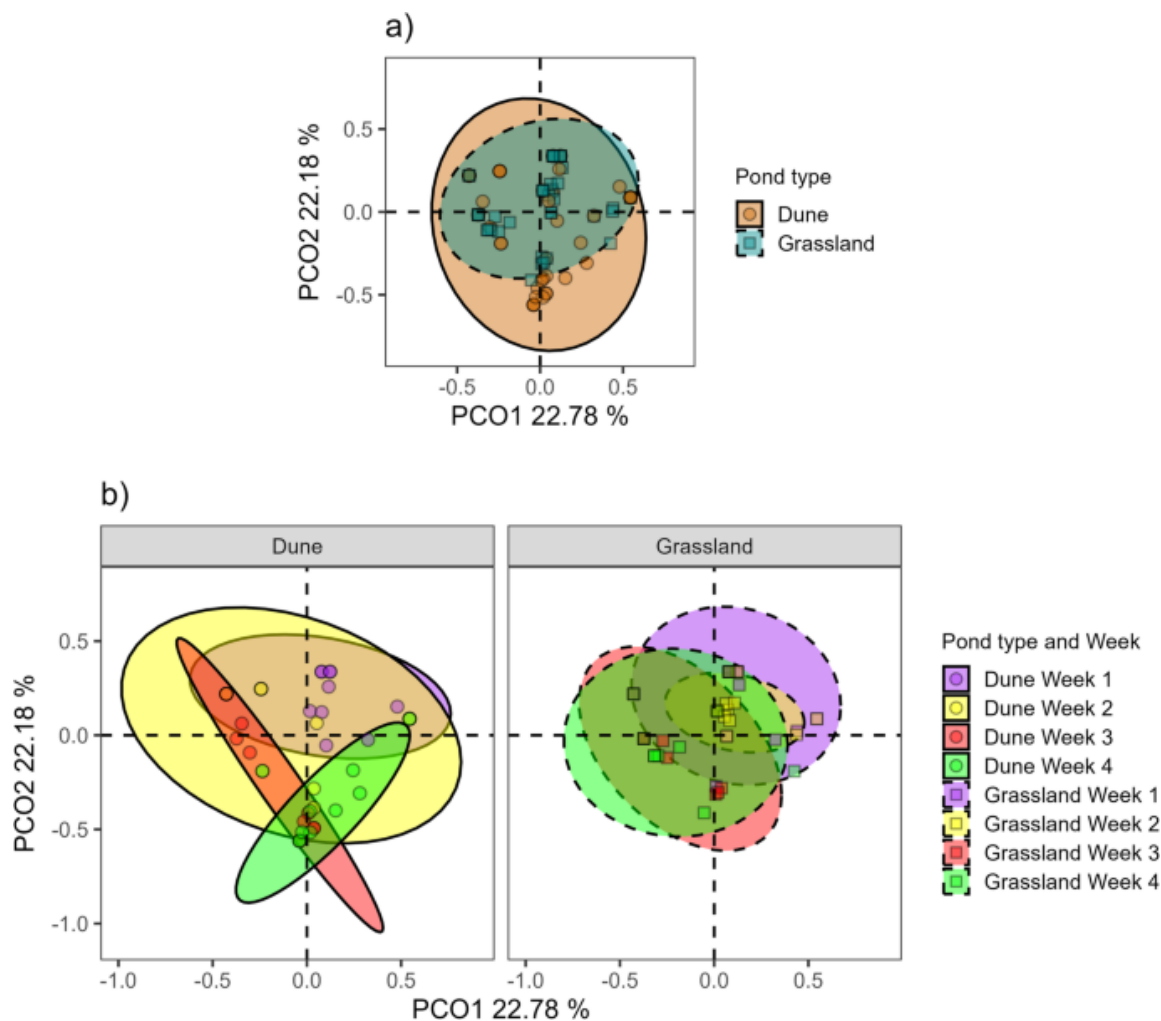


Fig. 5. a) PCoA plot showing the composition of invertebrate hatchlings and their variation between dune and grassland ponds, and b) among the weeks of the incubation experiment (Weeks 1 to 4).

Tardigrades, Acari, and collembolans mostly emerged after the second week of hydration. Collembolans were found only in dune ponds, while tardigrades and Acari occurred in both dune and grassland ponds. Anostracans only hatched in the first week of hydration and conchostracans only hatched during the middle of the experiment in grassland ponds. Although ostracods and cladocerans – both in dune and grassland ponds – spread their hatchlings mostly after the first week of hydration, copepods only hatched in the final week of hydration. Nematodes, oligochaetes and bdelloid rotifers emerged throughout all weeks of the hydration experiment in both dune and grassland ponds. The Indicator Species Analysis summarizes hatchling patterns in both grassland and dune ponds throughout the incubation weeks (Table 3), highlighting that while some taxa emerged later and exclusively from dune pond sediments (e.g., Aelosomatidae sp. 2), others were associated with grassland ponds, hatching from mid to late in the sediment hydration period (e.g., *Simocephalus* cf. *serrulatus*). Additionally, some taxa occurred in both dune and grassland ponds, either at the beginning (Platyhelminthes), at the end (Acari), or throughout nearly the entire hydration period (Nematoda, *Adineta* sp.).

Discussion

In this study we analyzed the hatching of dormant invertebrates over time in sediments from temporary ponds with different hydrological stability (grassland and dune ponds). Our results showed that sediments from dune ponds had a lower concentration of organic matter and lower hydrological stability when compared to grassland ponds. Some studies indicated that sandy sediments (with large particles) associated with low amounts of organic matter reduce the surface water retention capacity of intermittent wetlands throughout the year (Penatti and Almeida 2012; Mitsch and Gosselink 2015). The lower hydrological stability and the higher frequency of drought events in dune ponds compared

to grassland ponds during the monitoring period may have contributed to the observed variations in their physical and chemical parameters.

Although the richness of invertebrate hatchlings was similar between the dune and grassland ponds, the composition did not, partially corroborating our first hypothesis that the richness and composition of hatchlings would be different among ponds with different hydrological stability. The similarity in richness may be attributed to a trade-off involving invertebrate taxa that were unique to each environment. Some species of rotifers (*Dipleuchlanis propatula* and *Euchlanis* sp.) and cladocerans (*Pleuroxus* sp., *Ovalona glabra* and *Ceriodaphnia quadrangula*) occurred only in dune ponds, and *Simocephalus* cf. *serrulatus* and *Leydigia striata* hatched only in grassland ponds. Several studies have shown that habitat characteristics influence the structure of dormant propagule banks of aquatic invertebrates (Garcia-Roger et al. 2006; Brendonck et al. 2017; Portinho et al. 2017; Stenert et al. 2017; Vargas et al. 2019; Chaparro et al. 2021; Freiry et al. 2021). The differences in habitat characteristics (granulometry, sediment organic matter and physical and chemical characteristics of the water) and hydrological stability may have been responsible for the composition dissimilarity of hatched invertebrate taxa between dune and grassland ponds.

More specifically, the hydrological variation between dune and grassland ponds may have influenced hatchling composition both directly (e.g., by affecting sediment conditions for hatching) and indirectly (through historical ecological processes or the assembly of the dormant bank). Hydrological stability can act as an environmental filter for certain taxa, while favoring others, particularly depending on their life cycle strategies and the time required to complete development after hatching (Brendonck et al., 2017). Shorter hydroperiods and greater surface water variability in dune ponds may result in more frequent cues to produce dormant stages, potentially favoring species capable of

responding rapidly to the specific stimuli of these habitats (Golladay et al., 1997; Stenert et al., 2017). However, other factors should not be ruled out as drivers of dissimilarity between dune and grassland ponds, such as dispersal, which is a key ecological process influencing the structure and dynamics of populations and communities in response to hydrological variability (Vanschoenwinkel et al. 2008; Brendonck et al. 2017).

The similarity in invertebrate richness between dune and grassland ponds over the experiment shows that the invertebrate taxa spread their hatchings throughout the flood cycle, regardless of pond hydrological stability. Spreading hatching over the flooding period is a fundamental strategy of aquatic organisms to endure extreme conditions in wetlands (Vanoverbeke and De Meester 2009). In unpredictable regions, dormant invertebrates and vertebrates can spread their hatchings over several floods (Pinceel et al. 2021; Pires et al. 2022; Weber et al. 2024). Furthermore, the spreading of propagule hatchings observed over time in both dune and grassland ponds can be seen as a strategy to avoid intra- and interspecific competition for natural resources (Jocqué et al. 2010; Pinceel et al. 2021).

The accumulated invertebrate richness over the experiment was similar between dune and grassland sediments, refuting our second hypothesis that more delayed hatching responses would be observed in dune than grassland ponds. These results also showed that the hatching of dormant stages of different invertebrate taxa was distributed over time. The timing of dormancy breaking is an important characteristic of intermittent ponds, as it determines colonization and population patterns (De Stasio 1990). Vendramin et al. (2023) found a significant increase of richness of zooplankton hatchlings on the middle-to-late phase (third and fourth weeks) compared to the beginning of the wet phase in intermittent wetlands of the Brazilian tropical semiarid. In contrast, Bandeira et al.

(2020) observed high peaks of microcrustacean hatchings at the beginning of the hydrological phase in intermittent wetlands of southern Brazil.

Some taxa (Anellida, Nematoda and Rotifera) hatched throughout the whole study period. Hoffmann et al. (2023) found a high abundance of Aeolossomatidae annelids in different depths of sediment in intermittent ponds. These organisms form desiccation-resistant cysts, possibly induced by adverse environmental conditions (Glasby et al. 2021). Nematodes can enter in a quiescent stage capable of surviving desiccation and possibly extremes temperatures (Poinar Jr. 2010). Monogononta rotifers showed slow responses to hydration, with no hatching at the beginning of the experiment, unlike Bdelloidea rotifers (*Adineta* sp.), which maintained hatching throughout the hydration period. The rapid hatching response of bdelloid rotifers in hydrated sediments has already been observed in studies of temporary ponds (Ricci 2001; Vendramin et al. 2023). These rotifers are anhydrobiotic organisms with morphological, physiological and biochemical adaptations to withstand the drastic loss of water and be able to recover their metabolism when rehydrated (Rebecchi 2013).

Crustaceans showed differences between the taxa analyzed. Anostracans only hatched in the first week of hydration. Some studies have shown that Anostraca nauplii were the first crustaceans to emerge from the rehydrated sediment in wetlands (Jocque et al. 2010; Vendramin et al. 2023). Ostracods hatched from the second week onwards and predominated in the final phase of the experiment, similarly to other studies carried out in intermittent ponds (Bandeira et al. 2020; Vendramin et al. 2023). Cladocerans emerged throughout the weeks of the experiment, but some taxa predominated in specific periods. Stenert et al. (2016) found differences in cladoceran hatching dynamics: while some species predominate at the beginning of hydration, others delay hatching over the weeks in ponds of southern Brazil. Tardigrades showed different hatching patterns between the

ponds studied. These organisms can exhibit both forms of dormancy (quiescence and diapause) which can occur separately or simultaneously to survive unpredictable habitats (Guidetti et al. 2011; Vendramin et al. 2022). While tardigrade quiescence includes anhydrobiosis, cryobiosis, and anoxybiosis, diapause involves strategies such as encystment, cyclomorphosis, and the production of resting eggs, reflecting a broad spectrum of dormancy mechanisms (Guidetti et al. 2011). Although we did not assess species-level identification or determine which specific structures were produced by the tardigrades found, some species within this group have been reported to exhibit bet-hedging strategies (Guidetti et al. 2011).

As potential limitations of the study, our results and conclusions may be influenced by the inherent biases associated with laboratory-controlled conditions, as various environmental cues affect hatching success (Freiry et al. 2021; Vendramin et al. 2023), including temperature and photoperiod, which signal specific seasons, as well as the risk of false flooding in unstable aquatic systems (Brendonck et al. 2017). Previous studies have demonstrated that the requirements for breaking dormancy in invertebrate resting stages are species-specific (Brendonck and De Meester 2003; Vandekerckhove et al. 2005). Furthermore, although the sampling frequency used during the incubation period may have significantly reduced the risk of parthenogenetic reproduction among hatched individuals, its occurrence cannot be definitively excluded from the experiment.

In conclusion, our results highlighted the structure and temporal dynamics of hatching from dormant stages of aquatic invertebrates in temporary ponds subjected to different levels of hydrological stability. Interdunal depressions represent highly unique and threatened ecosystems at risk of disappearance (Grootjans 2002; Stewart and Schriever 2023). Ponds located within these depressions harbored dormant invertebrate communities with richness comparable to those found in nearby grassland ponds, but with

distinct taxa composition. Furthermore, variations in hatching patterns among taxa suggest that, in both grassland and dune ponds of southernmost Brazil, aquatic invertebrates adopt bet-hedging strategies regardless of hydrological stability. We emphasize the need for future studies using sediment collected at different times to enable more robust inferences about the structure and dynamics of invertebrate hatching throughout the complete hydrological cycle of these temporary wetlands.

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References

- Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLD, Sparovek G (2013) Köppen's climate classification map for Brazil. *Meteorol Z* 22:711–728.
<https://doi.org/10.1127/0941-2948/2013/0507>
- Araújo LR, Lopes PM, Santangelo JM, Petry AC, Bozelli RL (2013) Zooplankton resting egg banks in permanent and temporary tropical aquatic systems. *Acta Limnol Bras* 25:235–245.
- Bandeira MGS, Martins KP, Palma-Silva C, Hepp LU, Albertoni EF (2020) Hydration time influences microcrustacean hatching in intermittent wetlands: in situ and ex situ

456 approaches. *Hydrobiologia* 847:3227–3245. [https://doi.org/10.1007/s10750-020-](https://doi.org/10.1007/s10750-020-04315-w)
 457 04315-w
 458 Bates D, Maechler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models
 459 using lme4. *J Stat Softw* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>
 460 Batzer D, Boix D (2016) An introduction to freshwater wetlands and their invertebrates.
 461 In: Batzer D, Boix D (eds) *Invertebrates in freshwater wetlands*. Springer, Cham, pp
 462 1–23. https://doi.org/10.1007/978-3-319-24978-0_1
 463 Brazil T, Caetano ACL, Vargas AL, Bozelli RL, Santangelo JM (2022) Desiccation
 464 increases the hatching of resting eggs of a freshwater calanoid copepod. *J Plankton*
 465 *Res* 44:273–277. <https://doi.org/10.1093/plankt/fbac008>
 466 Brendonck L, Riddoch BJ, van de Weghe V, van Dooren T (1998) The
 467 maintenance of egg banks in very short-lived pools: a case study with anostracans
 468 (Branchiopoda). *Adv. limnol.* 52:141-161
 469 Brendonck L, Meester LD (2003) Egg banks in freshwater zooplankton: evolutionary and
 470 ecological archives in the sediment. *Hydrobiologia* 491:65–84.
 471 <https://doi.org/10.1023/A:1024454905119>
 472 Brendonck L, Pinceel T, Ortells R (2017) Dormancy and dispersal as mediators of
 473 zooplankton population and community dynamics along a hydrological disturbance
 474 gradient in inland temporary pools. *Hydrobiologia* 796:201–222.
 475 <https://doi.org/10.1007/s10750-016-3006-1>
 476 Brock MA, Nielsen DL, Shiel RJ, Green JD, Langley JD (2003) Drought and aquatic
 477 community resilience: the role of eggs and seeds in sediments of temporary wetlands.
 478 *Freshw Biol* 48:1207–1218. <https://doi.org/10.1046/j.1365-2427.2003.01083.x>
 479 Cáceres CE (1997) Dormancy in invertebrates. *Invertebr Biol* 116:371–383.
 480 <https://doi.org/10.2307/3226870>

481 Chaparro G, Mariani M, Hein T (2021) Diversity of dormant and active zooplankton
 482 stages: Spatial patterns across scales in temperate riverine floodplains. *J Plankton Res*
 483 43:61–71. <https://doi.org/10.1093/plankt/fbaa063>
 484 Daré L, Henry R, Perbiche-Neves G, Castilho MCA, Portinho JL (2024) Diversity and
 485 composition of cladoceran egg bank in sediments and macrophyte roots from the
 486 littoral zone of tropical lakes. *Aquat Ecol* 58:571–581. [https://doi.org/10.1007/s10452-](https://doi.org/10.1007/s10452-024-10091-9)
 487 024-10091-9
 488 De Cáceres M, Legendre P (2009) Associations between species and groups of sites:
 489 indices and statistical inference. *Ecology* 90:3566–3574. [https://doi.org/10.1890/08-](https://doi.org/10.1890/08-1823.1)
 490 1823.1
 491 De Stasio BT (1990) The role of dormancy and emergence patterns in the dynamics of a
 492 freshwater zooplankton community. *Limnol Oceanogr* 35:1079–1090.
 493 <https://doi.org/10.4319/lo.1990.35.5.1079>
 494 Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a
 495 flexible asymmetrical approach. *Ecol Monogr* 67:345–366.
 496 [https://doi.org/10.1890/0012-9615\(1997\)067\[0345:SAAIST\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2)
 497 Elmoor-Loureiro LMA (1997) Manual de identificação de cladóceros límnicos do Brasil.
 498 Universa, Universidade Católica de Brasília, Brasília
 499 Elmoor-Loureiro LMA (2000) Brazilian cladoceran studies: where do we stand? *Nauplius*
 500 8:117–131.
 501 Eskinazi-Sant'anna EM, Pace ML (2018) The potential of the zooplankton resting-stage
 502 bank to restore communities in permanent and temporary waterbodies. *J Plankton Res*
 503 40:458–470. <https://doi.org/10.1093/plankt/fby023>
 504 Evans MEK, Dennehy JJ (2005) Germ banking: bet-hedging and variable release from
 505 egg and seed dormancy. *Q Rev Biol* 80:431–51. <https://doi.org/10.1086/498282>

506 Freiry RF, Pires MM, Gouvea A, Hoffmann PHO, Stenert C, Maltchik L (2021)
 507 Ecological correlates of the alpha and beta diversity of zooplankton hatchling
 508 communities in seasonal subtropical ponds. *Ecol Res* 36:464–477.
 509 <https://doi.org/10.1111/1440-1703.12213>
 510 García-Roger EM, Carmona MJ, Serra M (2006) A simple model relating habitat features
 511 to a diapause egg bank. *Limnol Oceanogr* 51:1542–1547.
 512 <https://doi.org/10.4319/lo.2006.51.3.1542>
 513 Golladay SW, Taylor BW, Palik BJ (1997) Invertebrate communities of forested limesink
 514 wetlands in southwest Georgia, USA: Habitat use and influence of extended
 515 inundation. *Wetlands*, 17:383-393. <https://doi.org/10.1007/BF03161428>.
 516 Glasby CJ, Erséus C, Martin P (2021) Annelids in extreme aquatic environments:
 517 diversity, adaptations and evolution. *Diversity* 13:98.
 518 <https://doi.org/10.3390/d13020098>
 519 Guidetti R, Altiero T, Rebecchi L (2011) On dormancy strategies in tardigrades. *J Insect*
 520 *Physiol* 57:567–576. <https://doi.org/10.1016/j.jinsphys.2011.03.003>
 521 Grootjans AP, Geelen HWT, Jansen AJM, Lammerts EJ (2002) Restoration of coastal
 522 dune slacks in the Netherlands. *Hydrobiologia* 478:181–203.
 523 <https://doi.org/10.1023/A:1021086832201>
 524 Hairston NG (1996) Zooplankton egg banks as biotic reservoirs in changing
 525 environments. *Limnol Oceanogr* 41:1087–1092.
 526 <https://doi.org/10.4319/lo.1996.41.5.1087>
 527 Hairston NG, Caceres CE (1996) Distribution of crustacean diapause: micro- and
 528 macroevolutionary pattern and process. *Hydrobiologia* 320:27–44.
 529 <https://doi.org/10.1007/BF00016802>

530 Hartig F (2024) DHARMA: Residual diagnostics for hierarchical (Multi-Level /
 531 Mixed) regression models. R package version 0.4.7. [https://CRAN.R-](https://CRAN.R-project.org/package=DHARMA)
 532 [project.org/package=DHARMA](https://CRAN.R-project.org/package=DHARMA)

533 Hoffmann PH, Adolfo A, Piu AG, Vendramin D, Martins L, Weber V, Maltchik L,
 534 Stenert C (2023) Invertebrate richness and hatching decrease with sediment depth in
 535 neotropical intermittent ponds. *Wetlands* 43:24. [https://doi.org/10.1007/s13157-023-](https://doi.org/10.1007/s13157-023-01675-6)
 536 [01675-6](https://doi.org/10.1007/s13157-023-01675-6)

537 R Core Team (2024) R: A language and environment for statistical computing. R
 538 Foundation for Statistical Computing, Vienna, Austria.

539 Iglesias C, Bonecker C, Brandão L, Crispim MC, Eskinazi-Sant'Anna EM, Gerhard M,
 540 Portinho JL, Maia-Barbosa P, Panarelli E, Santangelo JM (2016) Current knowledge
 541 of South American cladoceran diapause: A brief review. *Int Rev Hydrobiol* 101:91–
 542 104. <https://doi.org/10.1002/iroh.201501825>

543 Jocque M, Vanschoenwinkel B, Brendonck L (2010) Anostracan monopolisation of early
 544 successional phases in temporary waters? *Fundam Appl Limnol* 176:127–132.
 545 <https://doi.org/10.1127/1863-9135/2010/0176-0127>

546 Koste W (1978) Rotatoria. Gebrüder Bosntraeget, Stuttgart

547 Le S, Josse J, Husson F (2008) FactoMineR: An R package for multivariate analysis. *J*
 548 *Stat Softw* 25:1–18. <https://doi.org/10.18637/jss.v025.i01>

549 Lopes PM, Bozelli R, Bini LM, Santangelo JM, Declerck SAJ (2016) Contributions of
 550 airborne dispersal and dormant propagule recruitment to the assembly of rotifer and
 551 crustacean zooplankton communities in temporary ponds. *Freshw Biol* 61:658–669.
 552 <https://doi.org/10.1111/fwb.12735>

553 Martínez-Ruiz C, García-Roger EM (2015) Being first increases the probability of long
 554 diapause in rotifer resting eggs. *Hydrobiologia* 745:111–121.
 555 <https://doi.org/10.1007/s10750-014-2098-8>
 556 Mitsch W, Gosselink J (2015) *Wetlands*, 5th edn. John Wiley & Sons, Inc, Hoboken
 557 Nielsen DL, Smith FJ, Hillman TJ, Shiel RJ (2000) Impact of water regime and fish
 558 predation on zooplankton resting egg production and emergence. *J Plankton Res*
 559 22:433–446. <https://doi.org/10.1093/plankt/22.3.433>
 560 Nielsen DL, Podnar K, Watts RJ, Wilson AL (2013) Empirical evidence linking increased
 561 hydrologic stability with decreased biotic diversity within wetlands. *Hydrobiologia*
 562 708:81–96. <https://doi.org/10.1007/s10750-011-0989-5>
 563 Panarelli EA, Casanova S, Henry (2008) The role of resting eggs in the recovery of
 564 zooplankton community in a marginal lake of the Paranapanema River (São Paulo,
 565 Brazil), after a long drought period. *Limnologica* 20:75–90
 566 Penatti NC, Almeida TIRD (2012) Subdivision of Pantanal quarternary wetlands:
 567 MODIS NDVI time-series in the indirect detection of sediments granulometry. *Int.*
 568 *Arch. Photogramm. Remote Sens Spat Inf Sci XXXIX-B8*:311–316
 569 Pinceel T, Buschke F, Geerts A, Vanoverbeke J, Brendonck L, Vanschoenwinkel B
 570 (2021) An empirical confirmation of diversified bet hedging as a survival strategy in
 571 unpredictably varying environments. *Ecology* 102:e03496.
 572 <https://doi.org/10.1002/ecy.3496>
 573 Pires MM, Vendramin D, Medeiros ESF, Stenert C, Batzer DP, Maltchik L (2023) Bet-
 574 hedgers commit to the hedge: Zooplankton in ephemeral semiarid wetlands of tropical
 575 Brazil that widely spread risk. *Ecology* 104:e4014. <https://doi.org/10.1002/ecy.4014>

576 Poinar Jr GO (2010) Nematoda and Nematomorpha. In: Thorp JH, Covich AP (eds)
 577 Ecology and classification of freshwater invertebrates of North America, 3rd edn.
 578 Academic Press, San Diego, pp 237–276

579 Portinho JL, Nielsen DL, Ning N, Paul W, Nogueira M (2017) Spatial variability of
 580 aquatic plant and microfaunal seed and egg bank communities within a forested
 581 floodplain system of a temperate Australian river. *Aquat Sci* 79:515–527.
 582 <https://doi.org/10.1007/s00027-016-0514-z>

583 Portinho JL, Perbiche-Neves G (2025) Effects of long-term desiccation on zooplankton
 584 resting egg banks from tropical lake sediments. *Fresh Biol* 70:e70037.
 585 <https://doi.org/10.1111/fwb.70037>.

586 Radzikowski J (2013) Resistance of dormant stages of planktonic invertebrates to adverse
 587 environmental conditions. *J Plankton Res* 35:707–723.
 588 <https://doi.org/10.1093/plankt/fbt032>

589 Rambo B (2000) A fisionomia do Rio Grande do Sul: ensaio de monografia natural.
 590 Unisinos, São Leopoldo

591 Rebecchi L, Altiero T, Guidetti R (2007) Anhydrobiosis: the extreme limit of desiccation
 592 tolerance. *Invertebrate surviv. j.* 4:65-81.

593 Rebecchi L (2013) Dry up and survive: the role of antioxidant defences in anhydrobiotic
 594 organisms. *J Limnol* 72:62–72. <https://doi.org/10.4081/jlimnol.2013.s1.e8>

595 Ricci C (2001) Dormancy patterns in rotifers. *Hydrobiologia* 446:1–11.
 596 <https://doi.org/10.1023/A:1017548418201>

597 Santangelo JM (2009) Produção, eclosão e implicações ecológicas e evolutivas dos
 598 estágios dormentes do zooplâncton. *Limnotemas*. Sociedade Brasileira de Limnologia,
 599 Rio de Janeiro

600 Schröder T (2005) Diapause in monogonont rotifers. *Hydrobiologia* 546:291–306.
601 <https://doi.org/10.1007/s10750-005-4235-x>

602 Seeliger U (1998) O sistema das dunas costeiras frontais. In: Seeliger U, Odebrecht C,
603 Castello JP (eds) Os ecossistemas costeiro e marinho do extremo Sul do Brasil.
604 Ecoscientia, Rio Grande, pp 179–184

605 Sousa FDR, Elmoo-Loureiro LMA (2019) Identification key for the Brazilian genera and
606 species of Aloninae (Crustacea, Branchiopoda, Anomopoda, Chydoridae). *Pap*
607 *Avulsos Zool* 59:e20195924.

608 Stenert C, Ehlert B, Ávila AC, Sousa FDR, Esquinatti FM, Batzer DP, Maltchik L (2016)
609 Dormant propagule banks of aquatic invertebrates in ponds invaded by exotic pine
610 species in southern Brazil. *Mar Freshw Res* 68:954–963.
611 <https://doi.org/10.1071/MF16067>

612 Stenert C, Wüsth R, Pires MM, Freiry RF, Nielsen D, Maltchik L (2017) Composition of
613 cladoceran dormant stages in intermittent ponds with different hydroperiod lengths.
614 *Ecol Res* 32:921–930. <https://doi.org/10.1007/s11284-017-1498-4>

615 Stewart NA, Schriever TA (2023) Local environmental conditions influence species
616 replacement in Great Lakes interdunal wetland macroinvertebrate communities.
617 *Freshw Biol* 68:46–60. <https://doi.org/10.1111/fwb.14008>

618 Tuytens K, Vanschoenwinkel B, Waterkeyn A, Brendonck L (2014) Predictions of
619 climate change infer increased environmental harshness and altered connectivity in a
620 cluster of temporary pools. *Freshw Biol* 59:955–968.
621 <https://doi.org/10.1111/fwb.12319>

622 Vandekerckhove J, Declerck S, Jeppesen E, Conde-Porcuna JM, Brendonck L, De Meester
623 L (2005) Dormant propagule banks integrate spatio-temporal heterogeneity in

624 cladoceran communities. *Oecologia* 142:109–116. <https://doi.org/10.1007/s00442->
 625 005-0020-9
 626 Vanoverbeke J, Meester LD (2009) Within season short-term hatching delays suggest
 627 risk-spreading behaviour in populations of the freshwater cladoceran daphnia.
 628 *Ecoscience* 16:441–451. <https://doi.org/10.2980/16-4-3254>
 629 Vanschoenwinkel B, Gielen S, Seaman MT, Brendonck L (2008) Any way the wind
 630 blows – frequent wind dispersal drives species sorting in ephemeral aquatic habitats.
 631 *Oikos* 117:125–134.
 632 Vargas AL, Santangelo JM, Bozelli RL (2019) Recovery from drought: Viability and
 633 hatching patterns of hydrated and desiccated zooplankton resting eggs. *Int Rev*
 634 *Hydrobiol* 104:26–33. <https://doi.org/10.1002/iroh.201801977>
 635 Vargas AL, Brazil T, Santangelo JM, Bozelli RL (2024) Long-term droughts change the
 636 hatching patterns of zooplankton resting eggs from permanent and temporary lakes.
 637 *Freshw Biol* 69:635–644. <https://doi.org/10.1111/fwb.14234>
 638 Vendramin D, Pires MM, Freiry RF, Schneider AEB, Martins L, Medeiros ESF, Rocha
 639 O, Stenert C, Maltchik L (2022) Hatching dynamics of invertebrate dormant stages in
 640 temporary ponds are influenced by multiple hydrations. *Freshw Sci* 41:143–152.
 641 <https://doi.org/10.1086/719129>
 642 Vendramin D, Pires MM, Medeiros ESF, Stenert C, Maltchik L (2023) Life finds a way:
 643 Hatching dynamics of zooplankton dormant stages in intermittent wetlands from the
 644 Brazilian tropical semiarid. *J Arid Environ* 212:104949.
 645 <https://doi.org/10.1016/j.jaridenv.2023.104949>
 646 Wickham H (2016) *ggplot2: Elegant graphics for data analysis*. Springer-Verlag, New
 647 York

648 Williams DD (2006) The biology of temporary waters. Oxford University Press, New
649 York

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Conflict of interest/Competing Interests

The authors declare no conflict of interest regarding this publication. The authors have no relevant financial or non-financial interests to disclose.

Author contributions

João Afonso Poester-Carvalho, Leonardo Maltchik and Cristina Stenert assisted with conceptualization, methodology, writing, review and editing. João Afonso Poester-Carvalho and Cristina Stenert performed laboratory procedures and statistical analysis and visualization. João Afonso Poester-Carvalho and Raquel Fontoura Freiry performed specimen identification. Leonardo Maltchik and Cristina Stenert acquired funding for the project.

Data Availability

The datasets generated during the current study are available from the corresponding author on reasonable request.

Code Availability

Not applicable.

Ethics approval

676 We declare that data collection complied with the current Brazilian environmental laws
677 (SISBIO 45558).

Table 1. Mean and standard deviation of the environmental variables obtained for each pond. Pond (G = grassland, D = dune), VC (coefficient of variation of flooding surface area), ORP (oxidation reduction potential), DO (dissolved oxygen) and TDS (total dissolved solids).

Pond	Organic matter (%)	VC (%)	Number of drought events	pH	Temperature (°C)	ORP (mV)	Conductivity (mS/cm ⁻¹)	Turbidity (NTU)	DO (mg/L ⁻¹)	TDS (g/L ⁻¹)	Salinity (%)
G1	28.5	109.21	2 (Dec, Feb)	6.13 ± 0.37	20.17 ± 3.50	117.33 ± 87.00	2.19 ± 1.32	643.33 ± 235.49	6.34 ± 3.79	1.40 ± 0.85	0.11 ± 0.07
G2	19.1	81.05	1 (Feb)	5.67 ± 0.67	20.25 ± 3.50	344.25 ± 71.10	0.0552 ± 0.01	212.82 ± 273.90	8.02 ± 1.77	0.04 ± 0.01	0.00
G3	41.7	63.32	1 (Feb)	6.24 ± 0.82	20.95 ± 3.63	220.25 ± 62.40	0.172 ± 0.05	170.47 ± 75.75	4.13 ± 1.10	0.11 ± 0.03	0.01 ± 0.00
G4	9.4	106.12	2 (Dec, Feb)	6.11 ± 0.28	19.63 ± 4.80	270.33 ± 136.00	0.0923 ± 0.02	414.80 ± 309.86	8.55 ± 2.80	0.06 ± 0.01	0.003 ± 0.006
G5	8.4	154.70	3 (Jul, Dec, Feb)	6.70 ± 0.76	22.87 ± 3.66	141.00 ± 235.00	0.282 ± 0.07	419.45 ± 463.22	6.19 ± 3.99	0.18 ± 0.04	0.015 ± 0.007
D1	1.8	148.82	3 (Jul, Dec, Feb)	6.88 ± 0.18	22.69 ± 6.49	257.00 ± 46.70	0.351 ± 0.06	142.75 ± 162.99	5.41 ± 0.38	0.23 ± 0.04	0.015 ± 0.007
D2	0.7	135.51	2 (Dec, Feb)	7.82 ± 0.62	21.79 ± 7.60	295.00 ± 38.40	0.395 ± 0.03	28.33 ± 38.99	7.50 ± 0.25	0.26 ± 0.02	0.02 ± 0.00
D3	7.2	229.06	4 (Jul, Nov, Dec, Feb)	7.22	19.29	251.00	0.41	78.6	3.27	0.27	0.02
D4	0.2	147.84	2 (Dec, Feb)	7.00 ± 0.23	18.68 ± 5.7	307.66 ± 72.00	0.438 ± 0.08	70.77 ± 120.58	6.11 ± 2.35	0.28 ± 0.05	0.023 ± 0.006
D5	3.3	88.95	1 (Feb)	7.42 ± 0.94	21.47 ± 6.12	201.75 ± 132.00	0.494 ± 0.12	184.35 ± 207.80	7.74 ± 5.43	0.32 ± 0.08	0.025 ± 0.006

Table 2. Invertebrate hatchlings and respective sum of individuals per week (W) in both dune and grasslands ponds.

Phylum	Class	Subclass	Superorder	Order	Family	Taxa	Dune ponds				Grassland ponds			
							W1	W2	W3	W4	W1	W2	W3	W4
Anellida					Aelossomatidae	Aelossomatidae sp. 1	10	4	0	6	32	31	3	7
						Aelossomatidae sp. 2	0	9	72	282	3	3	0	2
Nematoda							46	12	7	1	108	80	51	23
Platyhelminthes	Turbellaria						10	3	0	0	12	10	0	0
Tardigrada							1	0	0	0	0	0	1	1
Rotifera	Bdelloidea					<i>Adineta</i> sp.	2	1	5	7	4	4	9	9
						Bdelloidea sp. 1	0	0	0	0	0	0	1	0
						Monogononta sp. 1	0	0	0	0	0	6	0	0
	Monogononta				Lecanidae	<i>Lecane bulla</i>	0	0	0	0	0	0	0	3
					Euchlanidae	<i>Dipleuchlanis propatula</i>	0	9	11	5	0	0	0	0
						<i>Euchlanis</i> sp.	0	0	1	0	0	0	0	0
Arthropoda	Arachnida		Acari				0	0	6	6	0	0	1	2
	Collembola						0	2	3	4	0	0	0	0
	Branchiopoda			Anostraca			0	0	0	0	13	0	0	0
				Anomopoda	Daphniidae	<i>Simocephalus</i> cf. <i>serrulatus</i>	0	0	0	0	0	6	23	10
						<i>Ceriodaphnia quadrangula</i>	1	6	0	0	0	0	0	0
					Chydoridae	<i>Ovalona glabra</i>	0	1	31	57	0	0	0	0
						<i>Pleuroxus</i> sp.	1	9	301	6	0	0	0	0
						<i>Leydigia striata</i>	0	0	0	0	2	1	3	0
				Conchostraca			0	0	0	0	0	4	1	0
	Ostracoda						0	6	40	13	0	0	0	2
	Copepoda			Harpacticoida			0	0	0	1	0	0	0	0
Total							71	62	477	388	174	145	93	59

Table 3. Summary output of the Indicator Species Analysis for dune and grassland ponds (pond type) and the respective weeks. The analysis allowed combinations of each pond type with the weeks of hydration.

Pond type		Weeks	Taxa	<i>IV</i>	<i>P</i> value
Dune		Week 3 + Week 4	Aelosomatidae sp. 2	0.640	0.005
		Week 2 + Week 3 + Week 4	Collembola	0.491	0.025
Grassland		Week 2	Monogononta sp. 1	0.447	0.045
		Week 3	<i>Leydigia striata</i>	0.437	0.040
		Week 2 + Week 3 + Week 4	<i>Simocephalus cf. serrulatus</i>	0.483	0.015
Both	Dune	Week 3 + Week 4 +	Acari	0.496	0.020
	Grassland	Week 4			
	Dune	Week 1 + Week 2 +	Tuberllaria (Platyhelminthes)	0.661	0.005
	Grassland	Week 1 + Week 2			
	Dune	Week 1 + Week 4 +	Aelossomatidae sp. 1	0.756	0.005
	Grassland	Week 1 + Week 2			
	Dune	Week 3 + Week 4 +	<i>Adineta</i> sp.	0.626	0.045
	Grassland	Week 2 + Week 3 + Week 4			
	Dune	Week 1 + Week 2 + Week 3 +	Nematoda	0.821	0.005
	Grassland	Week 1 + Week 2 + Week 3 + Week 4			

Figure legends

Fig. 1. Map showing the study area, highlighting the selected ponds. The coastal strip is characterized by the dune landscape, which is adjacent to the grassland landscape, toward the continent interior. G = Grassland ponds; D = Dune ponds.

Fig. 2. PCA biplot of the environmental variables measured in the ponds, separated by dune and grassland ponds.

Fig. 3. Richness of the sampling days in each hydration week, separated by dune and grassland ponds.

Fig. 4. Cumulative richness of all ponds, separated by dune and grassland ponds.

Fig. 5. a) PCoA plot showing the composition of invertebrate hatchlings and their variation between dune and grassland ponds, and b) among the weeks of the incubation experiment (Weeks 1 to 4).

CONSIDERAÇÕES FINAIS E PERSPECTIVAS

O presente trabalho trouxe novas informações sobre o papel da estabilidade hidrológica nas comunidades dormentes de invertebrados aquáticos em áreas úmidas no sul do Brasil. São encontrados padrões semelhantes de estrutura de comunidade e de eclosões nas matrizes ambientais (dunas e campos), independente da estabilidade hidrológica.

Não foram detectadas variações significativas de riqueza entre as comunidades de campos e dunas. Esse resultado é importante para a literatura sobre ambientes de dunas, demonstrando que esses ambientes abrigam uma diversidade semelhante aos ambientes de campo, mesmo apresentando condições mais severas de instabilidade hidrológica. Esse resultado também demonstra a importância dos estágios dormentes para a resiliência da comunidade nesse tipo de ambiente. Entretanto, variações nas comunidades dos ambientes com diferentes estabilidades hidrológicas foram detectadas, ainda que com diferenças individuais marcantes. As comunidades de dunas e campos podem ter sido influenciadas por outros fatores além da estabilidade hidrológica, como a dinâmica de dispersão das espécies e efeitos da paisagem.

Quanto à dinâmica de eclosões, trabalhos recentes, como Vendramin et al. (2023), Bandeira et al. (2020), e Eskinazi Sant'Anna & Pace (2018) demonstraram que a estrutura da comunidade de invertebrados varia ao longo do período de hidratação do sedimento em áreas com diferentes níveis de permanência hidrológica. Nossos resultados contribuem para essa literatura, mostrando que, em áreas intermitentes, que secam anualmente, os organismos variam nas estratégias de eclosão independentemente do nível de permanência hidrológica dessas áreas. Tanto nas áreas de dunas, como nas áreas de campos, a composição de espécies variou ao longo das semanas de hidratação, embora sem padrões distintos de riqueza acumulada, contradizendo nossa hipótese inicial de que áreas com maior instabilidade hidrológica apresentariam eclosões mais atrasadas.

Estudos futuros podem explorar mais aspectos da variação da comunidade ao longo do hidroperíodo, incorporando, por exemplo, outras facetas da diversidade, como as abordagens funcional e filogenética, que podem revelar outros padrões, como já testado por Rosa et al. (2021). Além disso, também é necessário explorar uma abordagem mecanicista, de como ocorre a sinalização para eclosões mais adiantadas ou atrasadas

nos organismos, bem como efeitos da instabilidade hidrológica na produção de estágios dormentes, algo ainda pouco estudado em áreas úmidas subtropicais.

REFERÊNCIAS

BANDEIRA, M. G. DA S.; MARTINS, K. P.; PALMA-SILVA, C.; HEPP, L. U.; ALBERTONI, E. F. Hydration time influences microcrustacean hatching in intermittent wetlands: in situ and ex situ approaches. **Hydrobiologia**, v. 847, n. 15, p. 3227–3245, 2020.

ESKINAZI-SANT'ANNA, E. M.; PACE, M. L. The potential of the zooplankton resting-stage bank to restore communities in permanent and temporary waterbodies. **Journal of Plankton Research**, v. 40, n. 4, p. 458–470, 2018.

ROSA, J.; PETSCH, D. K.; MARTENS, K.; HIGUTI, J. Species' traits and taxonomic distance can predict the hatching phenology of ostracod (Crustacea) resting eggs from tropical floodplain lakes. **International Review of Hydrobiology**, v. 106, n. 5 – 6, p. 226 – 238, 2021.

VENDRAMIN, D.; PIRES, M. M.; MEDEIROS, E. S. F.; STENERT, C.; MALTCHIK, L. Life finds a way: Hatching dynamics of zooplankton dormant stages in intermittent wetlands from the Brazilian tropical semiarid. **Journal of Arid Environments**, v. 212, 2023.



The Effects of Hydrological Stability on the Hatching Dynamics of Aquatic Invertebrates in Intermittent Ponds

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Abstract

Aquatic invertebrates including zooplanktonic and non-zooplanktonic taxa produce resting stages to persist during drought periods in temporary wetlands. These resting stages provide both resistance for these organisms during drought periods, as well as resilience with the arrival of the first floods. The hydrological stability of temporary wetlands influences the hatching pattern of dormant stages in the invertebrate community. Here, we compare the structure and hatching dynamics of dormant stages of the aquatic invertebrate community of temporary ponds with different levels of hydrological stability. A total of ten temporary ponds were selected - five dune ponds and five grassland ponds. A total of 1,469 invertebrates distributed among 22 taxa emerged from dune and grassland sediments. The total richness of hatchlings did not change between dune and grassland sediments and nor during the weeks of hydration. The differences in habitat characteristics and hydrological stability between dune and grassland ponds may have contributed to the variation in the composition of hatched invertebrates. Furthermore, our results showed that the hatching of dormant stages of the invertebrate community from temporary wetlands is spread throughout the entire surface water period, regardless of pond hydrological stability.

Keywords Dormancy · Dune slack · Pampa · Temporary wetlands · Zooplankton

Introduction

Many species of aquatic invertebrates inhabiting temporary wetlands possess physiological and behavioral adaptations to survive two hydrological extreme periods: flooding and drought (Williams 2006). Dormancy is a strategy adopted by these species to persist during drought periods, involving two key mechanisms: quiescence and diapause (Brendonck and De Meester 2003; Brendonck et al. 2017). Quiescence

occurs when the organism enters a hibernation state encased in a protective secretion to endure unfavorable environmental conditions and it can be observed in some species of rotifers and copepods. Diapause occurs when the organism produces resting eggs (via sexual reproduction) that hatch during favorable periods and it can be observed in species of Cladocera, Rotifera, Copepoda and Anostraca, among other aquatic invertebrates (Hairston 1996; Cáceres 1997; Schroder 2005; Santangelo 2009; Radzikowski 2013). For example, non-zooplanktonic aquatic invertebrates have different physiological and behavioral mechanisms to survive desiccation, such as dormant eggs or cysts observed in flatworms, oligochaetes, collembolans, mayflies, beetles, caddisflies and mosquitoes (Williams 2006). Besides, nematodes and tardigrades can also have a dormant stage in life cycle capable of surviving unpredictable habitats (Rebecchi et al. 2007; Guidetti et al. 2011; Vendramin et al. 2022).

Aquatic invertebrates produce resting stages that accumulate in the sediment, forming a dormant bank with strong generation overlap that can remain viable for many years (Hairston and Cáceres 1996; Brendonck and De Meester 2003; Brock et al. 2003). In this sense, the dormant bank acts as a genetic reservoir with important

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hydrological stability; more specifically, more delayed hatching responses are expected to occur equally across all invertebrate taxa in ponds with a lower hydrological stability over time (dunes) than ponds with higher hydrological stability (grasslands).

Materials and methods

Study Area

Sampling was conducted in the Coastal Plain of the Pampa region, in the southernmost portion of Brazil, Rio Grande municipality, Rio Grande do Sul State (Fig. 1). The region has a flat topography and moist subtropical climate. The absence of hills and the low altitude make the precipitation and temperature similar throughout the study area (Rambo 2000). This region presents a sand dune landscape with typical dune herbaceous vegetation, which is replaced by grassland landscape towards the inland continent (Seeliger 1998). Both dune and grassland landscapes are marked by small ponds formed by precipitation,

with variable surface flooding area throughout the year, including ponds that dried out from spring to late summer (Seeliger 1998). The annual precipitation ranges from 1,300 to 1,600 mm, uniformly distributed throughout the year, without a dry season (Alvares et al. 2013). The mean temperatures range between 14.6 °C in winter and 22.2 °C in summer, and the mean annual temperature is 17.5 °C (Alvares et al. 2013).

Sampling Design and Environmental Variables

Ten small ponds were selected among many others for the study during March 2024, five ponds in a dune landscape (henceforth 'dune ponds') and five ponds in a grassland landscape (henceforth 'grassland ponds') (Fig. 1). The selected ponds were isolated (had no connectivity between them), and the minimum distance between them was 700 m. All ponds had similar areas (<0.2 ha) and water depth <0.4 m. The following environmental variables were monitored at each pond during a period of nine months, from June 2024 to February 2025 (six times, in June, July, September, November, December, February)

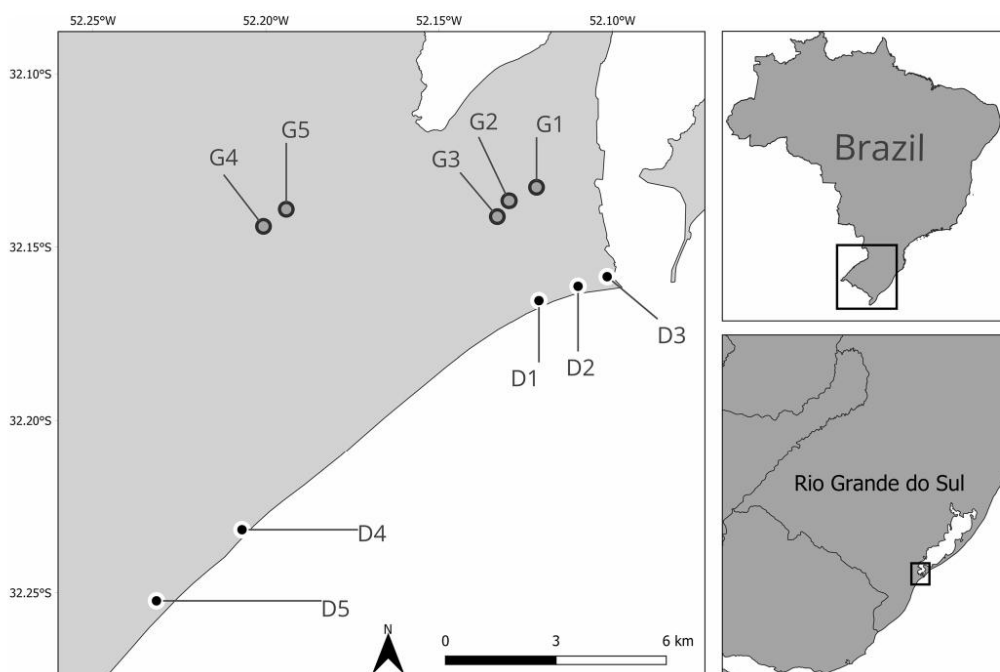


Fig. 1 Map showing the study area, highlighting the selected ponds. The coastal strip is characterized by the dune landscape, which is adjacent to the grassland landscape, toward the continent interior. G=Grassland ponds; D=Dune ponds

to provide a broader description and comparison of the variables between dune and grassland ponds: area (measured by walking around the perimeter of the wetland with a GPS), hydrological stability (measured by the variation of the surface flooding area over the monitoring period) and number of drought events in the monitored months; and water depth, pH, temperature, dissolved oxygen, electrical conductivity, water turbidity, total dissolved solids (TDS), oxidation reduction potential (ORP) and salinity, measured with a multiparameter water quality checker (HORIBA 207 U-22 Water Quality Checker). One sediment sample was collected in each pond for measurement of organic matter percentage in March 2024. The organic matter content was determined by drying the sediment at 60 °C for 24 h and burning it for 5 h in an oven at 550 °C.

Sediment Sampling, Incubation Experiment and Hatching Identification

In each pond, twelve sediment subsamples were randomly collected with a garden trowel (~100 g per subsample) from the topsoil layers (5-cm deep) in March 2024. The subsamples were pooled into a single sample per pond (~1 kg) in 5-L dark plastic bags. All grassland ponds and one dune pond contained water at the time of sediment sampling. In the laboratory, sediments from these ponds were dehydrated in a dark oven at 40 °C for at least 96 h to standardize desiccation, and subsequently homogenized.

The incubation experiment was conducted in May 2024, using 500 g of the homogenized sediment from each pond. Sediment was distributed into plastic trays (34 × 18 × 10 cm), each tray representing one pond. Distilled water was used to submerge the sediment, with a 2 cm water column (Hoffmann et al. 2023), which was maintained constant throughout the incubation by periodically adding distilled water. The experiment lasted 27 days (April 30th to May 27th) and the trays were kept at a temperature of 18 ± 3 °C (comparable with flooded field conditions recorded during the sampling season) and a photoperiod cycle of 12 h light/dark, using a climate-controlled room. Hatchlings were collected every 3 to 4 days, specifically on Mondays and Thursdays, using three standardized sweeps with a small hand-net (50 µm mesh size) adapted to the dimensions of the tray. This sampling procedure was used to minimize the chance of parthenogenetic reproduction (Brock et al. 2003; Daré et al. 2024). Hatchlings were isolated and counted under a stereomicroscope and transferred to microtubes with 80% ethanol. Unhatched dormant stages found were returned to the trays exactly as observed. Crustaceans and rotifers were identified to genus or species level when possible, using both specialized literature (Koste 1978; Elmoor-Loureiro 1997, 2000; Sousa and Elmoor-Loureiro 2019), consulting specialists

and with the assistance of a specialized website for the identification of cladocerans (<https://cladocera.wordpress.com/>).

Data Analysis

The hydrological stability of each pond was represented by the coefficient of variation (standard deviation divided by the mean) based on the variation of the surface flooding area over the monitoring period. The environmental variables of dune and grassland ponds were reduced by principal component analysis (PCA) based on the mean values of the water physical and chemical variables measured during the monitoring period and on a single value of the organic matter (since one sediment sample was collected from each pond) and coefficient of variation of flooding surface area. We conducted the PCA to visualize the most important environmental variables (limnological, sediment, and hydrological characteristics) that explain the differences between dune and grassland ponds. Additionally, differences in environmental variables between dune and grassland ponds were analyzed using a multivariate analysis of variance (MANOVA) based on the scores of the first two principal components (Axis 1 and Axis 2) from the PCA ordination.

We built a species accumulation curve to show the increase of the number of taxa for both dune and grassland ponds during the experiment. To compare the richness of hatchlings between dune and grassland ponds (Hypothesis 1) and the temporal hatching patterns among incubation weeks (Hypothesis 2), we used a Generalized Linear Mixed Model (GLMM). We categorized each sampling day for the corresponding week of the experiment (sampling days 1, 2 and 3 = week 1; sampling days 4 and 5 = week 2; sampling days 6 and 7 = week 3; and sampling days 8 and 9 = week 4). In the model, the richness is the response variable, while the hydration week and the pond type (dune and grassland) are the explanatory fixed effects, as well as an interaction effect. Each sampling day was accounted for as a random effect. We fitted the GLMM with Poisson distribution and log link and checked the assumptions of the model with diagnostic plots. We evaluated the significance of model terms using a Likelihood Ratio Test (LRT).

To assess variation in the taxa composition between dune and grassland ponds (Hypothesis 1) and among incubation weeks (Hypothesis 2), we used principal coordinate analysis (PCoA) and permutational multivariate analysis of variance (PERMANOVA) using the Jaccard distance matrix and 9,999 permutations to validate the model significance. We verified the dispersion of beta diversity between weeks, pond types (dune and grassland) and the combinations of both (weeks and pond types), using the betadisper method from vegan package (Oksanen et al. 2024).

The Indicator Species Analysis (IndVal; Dufrêne and Legendre 1997) was utilized to identify invertebrate taxa associated with each pond type and weeks of the incubation experiment. The statistical significance of the observed IV for each invertebrate taxa was assessed through 9,999 permutations. All analytical procedures were performed using the packages vegan (Oksanen et al. 2024), lme4 (Bates et al. 2015), DHAMRA (Hartig 2024), FactoMineR (Lê et al. 2008), ggplot2 (Wickham 2016) and indicpecies (De Cáceres and Legendre 2009) in R v 4.4.0 (R Core Team 2024).

Results

Environmental Variables

The PCA showed a separation between grassland and dune ponds based on environmental variables, which was further supported by the results of the multivariate analysis of variance (MANOVA) ($F_{1,8} = 10.837$, $P = 0.007$) (Fig. 2). The two principal components explained 42.73% and 22.1% of the data variation, respectively. The first component was

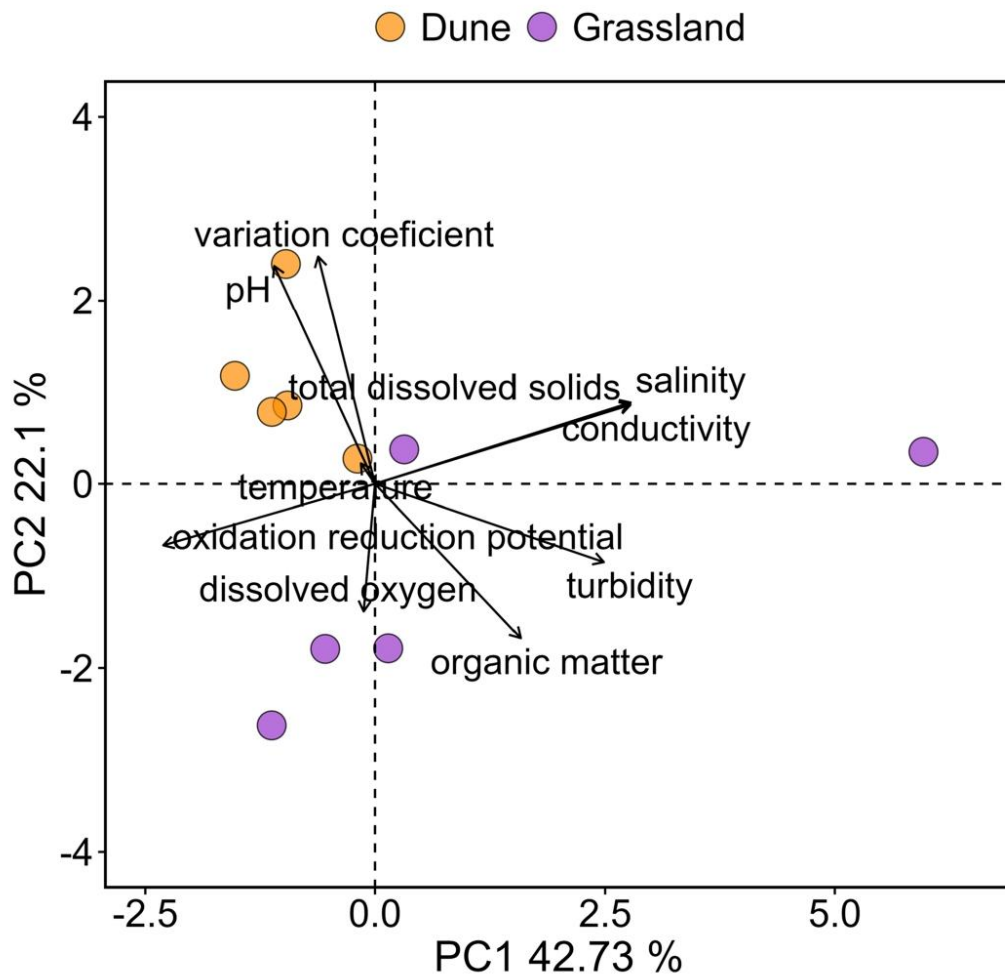


Fig. 2 PCA biplot of the environmental variables measured in the ponds, separated by dune and grassland ponds

positively correlated with conductivity, turbidity, total dissolved solids, salinity and organic matter percentage and negatively correlated with oxidation reduction potential. The second component was positively correlated with pH and coefficient of variation. Among the environmental variables, pH, temperature and oxidation reduction potential were higher in dune ponds, whereas turbidity, conductivity and sediment organic matter were higher in grassland ponds (Table 1; Fig. 2). The sediment organic matter ranged from 0.2 to 7.2% in dune ponds, and from 8.4 to 41.7% in grassland ponds (Table 1). The hydrological stability was lower in dune ponds compared to grassland ponds since the average of the coefficient of variation was 102.9% in grassland ponds and 150% in dune ponds. Besides, the grassland ponds had a lower mean number of droughts (1.8) than dune ponds (2.4) during the monitored period (Table 1).

Taxon Richness and Composition

A total of 1,469 invertebrates distributed among 22 taxa emerged from dune and grassland sediments, including zooplanktonic species of crustaceans (cladocerans, anostracans, conchostracans, ostracods and copepods), bdelloid and monogonont rotifers, and non-zooplanktonic invertebrate taxa such as collembolans, Acari, nematodes, oligochaetes, microturbellarians and tardigrades (Table 2). Eight taxa were found in both dune and grassland ponds. However, some taxa emerged exclusively from dune sediments (seven taxa), such as collembolans, the monogonont rotifers *Dipleuchlanis propatula* and *Euchlanis* sp., the harpacticoid copepods and the cladocerans *Pleuroxus* sp., *Ovalona glabra* and *Ceriodaphnia quadrangula*. Some invertebrate taxa occurred only in sediments rehydrated from grassland ponds (seven taxa), including monogonont and bdelloid rotifers, anostracans, conchostracans and the cladocerans *Simocephalus* cf. *serrulatus* and *Leydigia striata*.

The total richness of hatchlings did not change between dune and grassland sediments (GLMM, $LR\ Chisq=0.152$, $df=1$, $P=0.697$) nor during the weeks of hydration (GLMM, $LR\ Chisq=3.272$, $df=2$, $P=0.195$) (Fig. 3). No interaction between weeks and pond types was observed in invertebrate richness (GLMM, $LR\ Chisq=4.022$, $df=3$, $P=0.259$) (Fig. 3). The species accumulation curve showed that the increase of invertebrate taxa richness was similar and gradual between dune and grassland sediments during the sampling events of the experiment (Fig. 4).

The composition of invertebrate hatchlings varied between grassland and dune ponds ($R^2=0.036$, $F_{1,79}=3.693$, $P=0.001$), and among the weeks of the incubation experiment ($R^2=0.124$, $F_{3,79}=4.174$, $P=0.001$) (Fig. 5). There was an interaction between weeks and pond types ($R^2=0.053$, $F_{3,79}=1.806$, $P=0.025$), showing that the

Table 1 Mean and standard deviation of the environmental variables obtained for each pond. Pond (G=grassland, D=dune), VC (coefficient of variation of flooding surface area), ORP (oxidation reduction potential), DO (dissolved oxygen) and IDS (total dissolved solids)

Pond	Organic matter (%)	VC (%)	Number of drought events	pH	Temperature (°C)	ORP (mV)	Conductivity (mS/cm ⁻¹)	Turbidity (NTU)	DO (mg/L ⁻¹)	TDS (g/L ⁻¹)	Salinity (‰)
G1	28.5	109.21	2 (Dec, Feb)	6.13±0.37	20.17±3.50	117.33±87.00	2.19±1.32	643.33±235.49	6.34±3.79	1.40±0.85	0.11±0.07
G2	19.1	81.05	1 (Feb)	5.67±0.67	20.25±3.50	344.25±71.10	0.052±0.01	212.82±273.90	8.02±1.77	0.04±0.01	0.00
G3	41.7	63.32	1 (Feb)	6.24±0.82	20.95±3.63	220.25±62.40	0.172±0.05	170.47±75.75	4.13±1.10	0.11±0.03	0.01±0.00
G4	9.4	106.12	2 (Dec, Feb)	6.11±0.28	19.63±4.80	270.33±136.00	0.0923±0.02	414.80±309.86	8.55±2.80	0.06±0.01	0.003±0.006
G5	8.4	154.70	3 (Jul, Dec, Feb)	6.70±0.76	22.87±3.66	141.00±235.00	0.282±0.07	419.45±463.22	6.19±3.99	0.18±0.04	0.015±0.007
D1	1.8	148.82	3 (Jul, Dec, Feb)	6.88±0.18	22.69±6.49	257.00±46.70	0.351±0.06	142.75±162.99	5.41±0.38	0.23±0.04	0.015±0.007
D2	0.7	135.51	2 (Dec, Feb)	7.82±0.62	21.79±7.60	295.00±38.40	0.395±0.03	28.33±38.99	7.50±0.25	0.26±0.02	0.02±0.00
D3	7.2	229.06	4 (Jul, Nov, Dec, Feb)	7.22	19.29	251.00	0.41	78.6	3.27	0.27	0.02
D4	0.2	147.84	2 (Dec, Feb)	7.00±0.23	18.68±5.7	307.66±72.00	0.438±0.08	70.77±120.58	6.11±2.35	0.28±0.05	0.023±0.006
D5	3.3	88.95	1 (Feb)	7.42±0.94	21.47±6.12	201.75±132.00	0.494±0.12	184.35±207.80	7.74±5.43	0.32±0.08	0.025±0.006

composition changed between grassland and dune ponds over the experiment. The composition variation between dune and grassland ponds was more affected by internal dispersion of beta diversity, as shown by the Betadisper analysis ($F_{1,85} = 7.981$, $P=0.014$, Fig. 5a). Similarly, the composition variation among weeks was also affected by internal dispersion in both dune and grassland ponds ($F_{3,83} = 3.890$, $P=0.010$, Figure 5b). Dune ponds showed greater visual segregation than grassland ponds in the composition of invertebrate hatchlings between the initial (early hatching) and final weeks (delayed hatching) of the experiment, which may be related to the interaction effect observed in the PERMANOVA (Fig. 5b).

Tardigrades, Acari, and collembolans mostly emerged after the second week of hydration. Collembolans were found only in dune ponds, while tardigrades and Acari occurred in both dune and grassland ponds. Anostracans only hatched in the first week of hydration and conchostacans only hatched during the middle of the experiment in grassland ponds. Although ostracods and cladocerans – both in dune and grassland ponds – spread their hatchlings mostly after the first week of hydration, copepods only hatched in the final week of hydration. Nematodes, oligochaetes and bdelloid rotifers emerged throughout all weeks of the hydration experiment in both dune and grassland ponds. The Indicator Species Analysis summarizes hatchling patterns in both grassland and dune ponds throughout the incubation weeks (Table 3), highlighting that while some taxa emerged later and exclusively from dune pond sediments (e.g., Aelosomatidae sp. 2), others were associated with grassland ponds, hatching from mid to late in the sediment hydration period (e.g., *Simocephalus* cf. *serrulatus*). Additionally, some taxa occurred in both dune and grassland ponds, either at the beginning (Platyhelminthes), at the end (Acari), or throughout nearly the entire hydration period (Nematoda, *Adineta* sp.).

Discussion

In this study we analyzed the hatching of dormant invertebrates over time in sediments from temporary ponds with different hydrological stability (grassland and dune ponds). Our results showed that sediments from dune ponds had a lower concentration of organic matter and lower hydrological stability when compared to grassland ponds. Some studies indicated that sandy sediments (with large particles) associated with low amounts of organic matter reduce the surface water retention capacity of intermittent wetlands throughout the year (Penatti and Almeida 2012; Mitsch and Gosselink 2015). The lower hydrological stability and the higher frequency of drought events in dune ponds compared

to grassland ponds during the monitoring period may have contributed to the observed variations in their physical and chemical parameters.

Although the richness of invertebrate hatchlings was similar between the dune and grassland ponds, the composition did not, partially corroborating our first hypothesis that the richness and composition of hatchlings would be different among ponds with different hydrological stability. The similarity in richness may be attributed to a trade-off involving invertebrate taxa that were unique to each environment. Some species of rotifers (*Dipleuchlanis propatula* and *Euchlanis* sp.) and cladocerans (*Pleuroxus* sp., *Ovalona glabra* and *Ceriodaphnia quadrangula*) occurred only in dune ponds, and *Simocephalus* cf. *serrulatus* and *Leydigia striata* hatched only in grassland ponds. Several studies have shown that habitat characteristics influence the structure of dormant propagule banks of aquatic invertebrates (Garcia-Roger et al. 2006; Brendonck et al. 2017; Portinho et al. 2017; Stenert et al. 2017; Vargas et al. 2019; Chaparro et al. 2021; Freiry et al. 2021). The differences in habitat characteristics (granulometry, sediment organic matter and physical and chemical characteristics of the water) and hydrological stability may have been responsible for the composition dissimilarity of hatched invertebrate taxa between dune and grassland ponds.

More specifically, the hydrological variation between dune and grassland ponds may have influenced hatchling composition both directly (e.g., by affecting sediment conditions for hatching) and indirectly (through historical ecological processes or the assembly of the dormant bank). Hydrological stability can act as an environmental filter for certain taxa, while favoring others, particularly depending on their life cycle strategies and the time required to complete development after hatching (Brendonck et al. 2017). Shorter hydroperiods and greater surface water variability in dune ponds may result in more frequent cues to produce dormant stages, potentially favoring species capable of responding rapidly to the specific stimuli of these habitats (Golladay et al. 1997; Stenert et al. 2017). However, other factors should not be ruled out as drivers of dissimilarity between dune and grassland ponds, such as dispersal, which is a key ecological process influencing the structure and dynamics of populations and communities in response to hydrological variability (Vanschoenwinkel et al. 2008; Brendonck et al. 2017).

The similarity in invertebrate richness between dune and grassland ponds over the experiment shows that the invertebrate taxa spread their hatchlings throughout the flood cycle, regardless of pond hydrological stability. Spreading hatching over the flooding period is a fundamental strategy of aquatic organisms to endure extreme conditions in wetlands (Vanoverbeke and De Meester 2009). In unpredictable

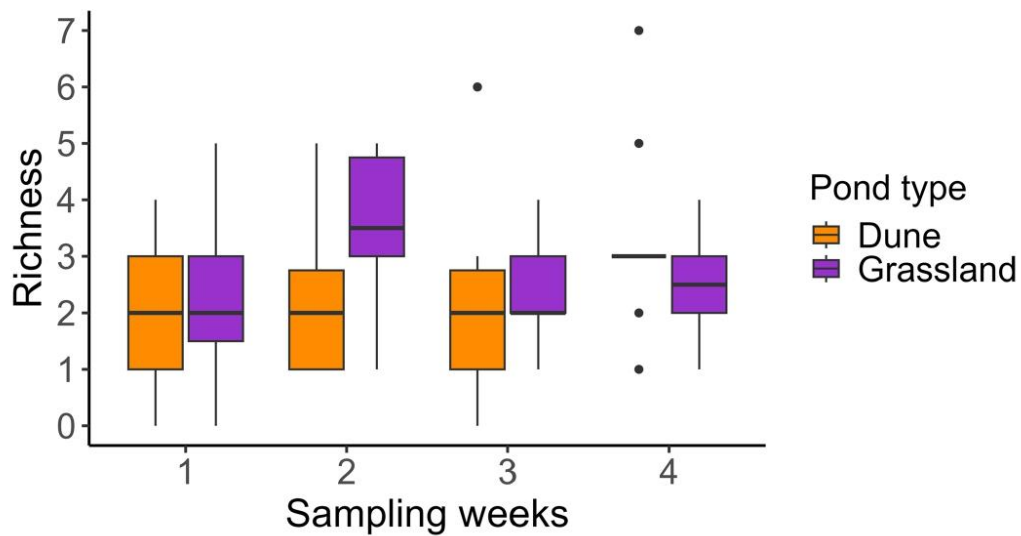


Fig. 3 Richness of the sampling days in each hydration week, separated by dune and grassland ponds

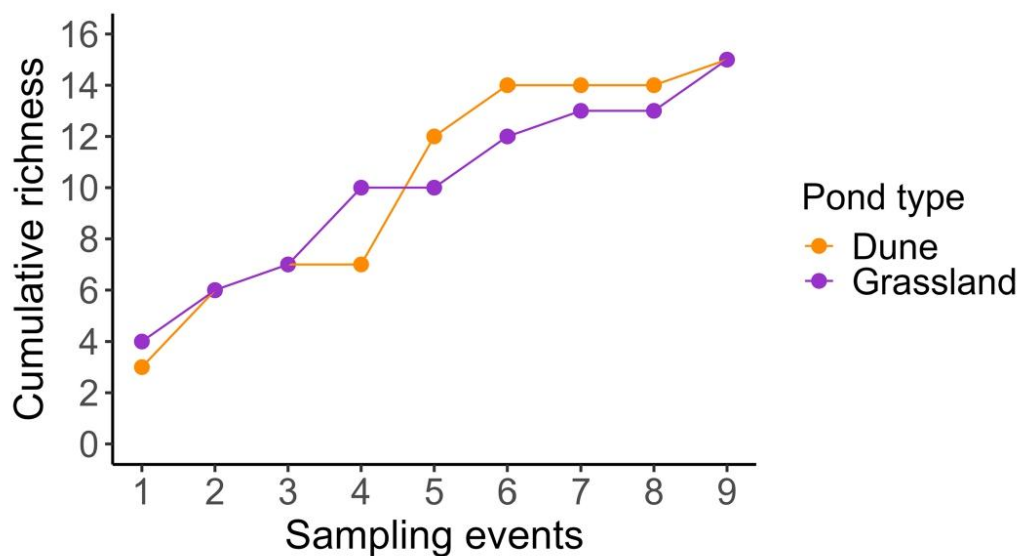


Fig. 4 Cumulative richness of all ponds, separated by dune and grassland ponds

regions, dormant invertebrates and vertebrates can spread their hatchings over several floods (Pinceel et al. 2021; Pires et al. 2023; Weber et al. 2025a,2025b). Furthermore, the spreading of propagule hatchings observed over time in both dune and grassland ponds can be seen as a strategy

to avoid intra- and interspecific competition for natural resources (Jocqué et al. 2010; Pinceel et al. 2021).

The accumulated invertebrate richness over the experiment was similar between dune and grassland sediments, refuting our second hypothesis that more delayed hatching

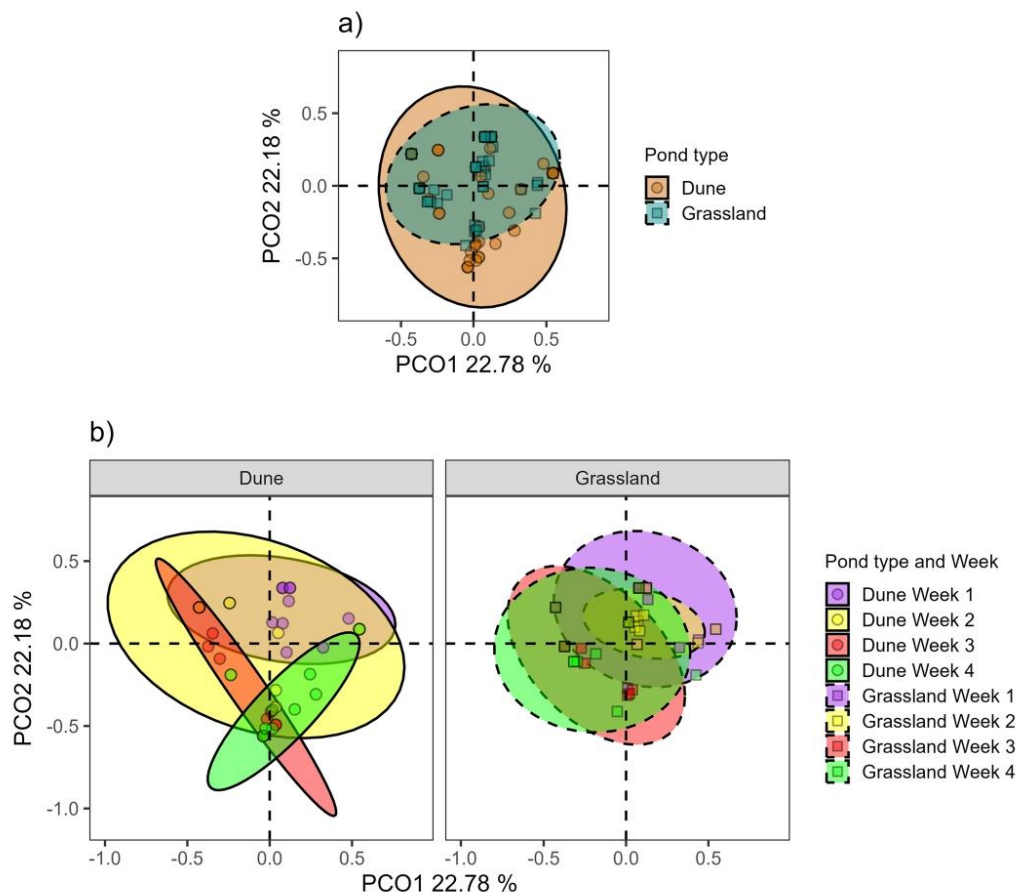


Fig. 5 (a) PCoA plot showing the composition of invertebrate hatchlings and their variation between dune and grassland ponds, and (b) among the weeks of the incubation experiment (Weeks 1 to 4)

responses would be observed in dune than grassland ponds. These results also showed that the hatching of dormant stages of different invertebrate taxa was distributed over time. The timing of dormancy breaking is an important characteristic of intermittent ponds, as it determines colonization and population patterns (De Stasio 1990). Vendramin et al. (2023) found a significant increase of richness of zooplankton hatchlings on the middle-to-late phase (third and fourth weeks) compared to the beginning of the wet phase in intermittent wetlands of the Brazilian tropical semiarid. In contrast, Bandeira et al. (2020) observed high peaks of microcrustacean hatchlings at the beginning of the hydrological phase in intermittent wetlands of southern Brazil.

Some taxa (Anellida, Nematoda and Rotifera) hatched throughout the whole study period. Hoffmann et al. (2023) found a high abundance of Aeolosomatidae annelids in different depths of sediment in intermittent ponds. These organisms form desiccation-resistant cysts, possibly induced by adverse environmental conditions (Glasby et al. 2021). Nematodes can enter in a quiescent stage capable of surviving desiccation and possibly extremes temperatures (Poinar Jr 2010). Monogononta rotifers showed slow responses to hydration, with no hatching at the beginning of the experiment, unlike Bdelloidea rotifers (*Adineta* sp.), which maintained hatching throughout the hydration period. The rapid hatching response of bdelloid rotifers in hydrated sediments has already been observed in studies of temporary ponds

Table 3 Summary output of the indicator species analysis for Dune and grassland ponds (pond type) and the respective weeks. The analysis allowed combinations of each pond type with the weeks of hydration

Pond type	Weeks	Taxa	IV	P value
Dune	Week 3 + Week 4	Aelosomatidae sp. 2	0.640	0.005
	Week 2 + Week 3 + Week 4	Collembola	0.491	0.025
Grassland	Week 2	Monogononta sp. 1	0.447	0.045
	Week 3	<i>Leydigia striata</i>	0.437	0.040
	Week 2 + Week 3 + Week 4	<i>Simocephalus cf. serrulatus</i>	0.483	0.015
	Week 3 + Week 4 +	Acari	0.496	0.020
Both	Dune	Tubellaria (Platyhelminthes)	0.661	0.005
	Grassland			
	Dune	Aelosomatidae sp. 1	0.756	0.005
	Grassland			
	Dune	<i>Adineta</i> sp.	0.626	0.045
	Grassland			
	Dune	Nematoda	0.821	0.005
	Grassland			
	Dune	Week 1 + Week 2 +		
	Grassland			

(Ricci 2001; Vendramin et al. 2023). These rotifers are anhydrobiotic organisms with morphological, physiological and biochemical adaptations to withstand the drastic loss of water and be able to recover their metabolism when rehydrated (Rebecchi 2013).

Crustaceans showed differences between the taxa analyzed. Anostracans only hatched in the first week of hydration. Some studies have shown that Anostraca nauplii were the first crustaceans to emerge from the rehydrated sediment in wetlands (Jocque et al. 2010; Vendramin et al. 2023). Ostracods hatched from the second week onwards and predominated in the final phase of the experiment, similarly to other studies carried out in intermittent ponds (Bandeira et al. 2020; Vendramin et al. 2023). Cladocerans emerged throughout the weeks of the experiment, but some taxa predominated in specific periods. Stenert et al. (2016) found differences in cladoceran hatching dynamics: while some species predominate at the beginning of hydration, others delay hatching over the weeks in ponds of southern Brazil. Tardigrades showed different hatching patterns between the ponds studied. These organisms can exhibit both forms of dormancy (quiescence and diapause) which can occur separately or simultaneously to survive unpredictable habitats (Guidetti et al. 2011; Vendramin et al. 2022). While tardigrade quiescence includes anhydrobiosis, cryobiosis, and anoxybiosis, diapause involves strategies such as encystment, cyclomorphosis, and the production of resting eggs, reflecting a broad spectrum of dormancy mechanisms (Guidetti et al. 2011). Although we did not assess species-level identification or determine which specific structures were produced by the tardigrades found, some species within this group have been reported to exhibit bet-hedging strategies (Guidetti et al. 2011).

As potential limitations of the study, our results and conclusions may be influenced by the inherent biases associated with laboratory-controlled conditions, as various

environmental cues affect hatching success (Freiry et al. 2021; Vendramin et al. 2023), including temperature and photoperiod, which signal specific seasons, as well as the risk of false flooding in unstable aquatic systems (Brendonck et al. 2017). Previous studies have demonstrated that the requirements for breaking dormancy in invertebrate resting stages are species-specific (Brendonck and De Meester 2003; Vandekerckhove et al. 2005). Furthermore, although the sampling frequency used during the incubation period may have significantly reduced the risk of parthenogenetic reproduction among hatched individuals, its occurrence cannot be definitively excluded from the experiment.

In conclusion, our results highlighted the structure and temporal dynamics of hatching from dormant stages of aquatic invertebrates in temporary ponds subjected to different levels of hydrological stability. Interdunal depressions represent highly unique and threatened ecosystems at risk of disappearance (Grootjans 2002; Stewart and Schriever 2023). Ponds located within these depressions harbored dormant invertebrate communities with richness comparable to those found in nearby grassland ponds, but with distinct taxa composition. Furthermore, variations in hatching patterns among taxa suggest that, in both grassland and dune ponds of southernmost Brazil, aquatic invertebrates adopt bet-hedging strategies regardless of hydrological stability. We emphasize the need for future studies using sediment collected at different times to enable more robust inferences about the structure and dynamics of invertebrate hatching throughout the complete hydrological cycle of these temporary wetlands.

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Author Contributions João Afonso Poester-Carvalho, Leonardo Maltchik and Cristina Stenert assisted with conceptualization, methodology, writing, review and editing. João Afonso Poester-Carvalho and Cristina Stenert performed laboratory procedures and statistical analysis and visualization. João Afonso Poester-Carvalho and Raquel Fontoura Freiry performed specimen identification. Leonardo Maltchik and Cristina Stenert acquired funding for the project.

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Data Availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Code Availability Not applicable.

Declarations

Conflict of interest The authors declare no conflict of interest regarding this publication. The authors have no relevant financial or non-financial interests to disclose.

Ethics Approval We declare that data collection complied with the current Brazilian environmental laws (SISBIO 45558).

References

- Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLD, Sparovek G (2013) Köppen's climate classification map for Brazil. *Meteorol Z* 22:711–728. <https://doi.org/10.1127/0941-2948/2013/0507>
- Araújo LR, Lopes PM, Santangelo JM, Petry AC, Bozelli RL (2013) Zooplankton resting egg banks in permanent and temporary tropical aquatic systems. *Acta Limnol Bras* 25:235–245
- Bandeira MGS, Martins KP, Palma-Silva C, Hepp LU, Albertoni EF (2020) Hydration time influences microcrustacean hatching in intermittent wetlands: in situ and ex situ approaches. *Hydrobiologia* 847:3227–3245. <https://doi.org/10.1007/s10750-020-04315-w>
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear Mixed-Effects models using lme4. *J Stat Softw* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>
- Batzer D, Boix D (2016) An introduction to freshwater wetlands and their invertebrates. In: Batzer D, Boix D (eds) *Invertebrates in freshwater wetlands*. Springer, Cham, pp 1–23. https://doi.org/10.1007/978-3-319-24978-0_1
- Brazil T, Caetano ACL, Vargas AL, Bozelli RL, Santangelo JM (2022) Desiccation increases the hatching of resting eggs of a freshwater calanoid copepod. *J Plankton Res* 44:273–277. <https://doi.org/10.1093/plankt/fba008>
- Brendonck L, Meester LD (2003) Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment. *Hydrobiologia* 491:65–84. <https://doi.org/10.1023/A:1024454905119>
- Brendonck L, Riddoch BJ, van de Weghe V, van Dooren T (1998) The maintenance of egg banks in very short-lived pools: a case study with anostracans (Branchiopoda). *Adv Limnol* 52:141–161
- Brendonck L, Pinceel T, Ortells R (2017) Dormancy and dispersal as mediators of zooplankton population and community dynamics along a hydrological disturbance gradient in inland temporary pools. *Hydrobiologia* 796:201–222. <https://doi.org/10.1007/s10750-016-3006-1>
- Brock MA, Nielsen DL, Shiel RJ, Green JD, Langley JD (2003) Drought and aquatic community resilience: the role of eggs and seeds in sediments of temporary wetlands. *Freshw Biol* 48:1207–1218. <https://doi.org/10.1046/j.1365-2427.2003.01083.x>
- Cáceres CE (1997) Dormancy in invertebrates. *Invertebr Biol* 116:371–383. <https://doi.org/10.2307/3226870>
- Chaparro G, Mariani M, Hein T (2021) Diversity of dormant and active zooplankton stages: Spatial patterns across scales in temperate riverine floodplains. *J Plankton Res* 43:61–71. <https://doi.org/10.1093/plankt/fbaa063>
- Daré L, Henry R, Perbiche-Neves G, Castilho MCA, Portinho JL (2024) Diversity and composition of Cladoceran egg bank in sediments and macrophyte roots from the Littoral zone of tropical lakes. *Aquat Ecol* 58:571–581. <https://doi.org/10.1007/s10045-024-10091-9>
- De Cáceres M, Legendre P (2009) Associations between species and groups of sites: indices and statistical inference. *Ecology* 90:3566–3574. <https://doi.org/10.1890/08-1823.1>
- De Stasio BT (1990) The role of dormancy and emergence patterns in the dynamics of a freshwater zooplankton community. *Limnol Oceanogr* 35:1079–1090. <https://doi.org/10.4319/lo.1990.35.5.1079>
- Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol Monogr* 67:345–366. [https://doi.org/10.1890/0012-9615\(1997\)067\[0345:SAAIJ\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIJ]2.0.CO;2)
- Elmoor-Loureiro LMA (1997) Manual de identificação de Cladóceros límnicos do Brasil. Universa, Universidade Católica de Brasília, Brasília
- Elmoor-Loureiro LMA (2000) Brazilian Cladoceran studies: where do we stand? *Nauplius* 8:117–131
- Eskinazi-Sant'anna EM, Pace ML (2018) The potential of the zooplankton resting-stage bank to restore communities in permanent and temporary waterbodies. *J Plankton Res* 40:458–470. <https://doi.org/10.1093/plankt/fby023>
- Evans MEK, Dennehy JJ (2005) Germ banking: bet-hedging and variable release from egg and seed dormancy. *Q Rev Biol* 80:431–451. <https://doi.org/10.1086/498282>
- Freiry RF, Pires MM, Gouveia A, Hoffmann PHO, Stenert C, Maltchik L (2021) Ecological correlates of the alpha and beta diversity of zooplankton hatchling communities in seasonal subtropical ponds. *Ecol Res* 36:464–477. <https://doi.org/10.1111/1440-1703.12213>
- García-Roger EM, Carmona MJ, Serra M (2006) A simple model relating habitat features to a diapause egg bank. *Limnol Oceanogr* 51:1542–1547. <https://doi.org/10.4319/lo.2006.51.3.1542>
- Glasby CJ, Erséus C, Martin P (2021) Annelids in extreme aquatic environments: diversity, adaptations and evolution. *Diversity* 13:98. <https://doi.org/10.3390/d13020098>
- Golladay SW, Taylor BW, Palik BJ (1997) Invertebrate communities of forested Limesink wetlands in Southwest Georgia, USA: habitat use and influence of extended inundation. *Wetlands* 17:383–393. <https://doi.org/10.1007/BF03161428>
- Grootjans AP, Geelen HWT, Jansen AJM, Lammerts EJ (2002) Restoration of coastal Dune slacks in the Netherlands. *Hydrobiologia* 478:181–203. <https://doi.org/10.1023/A:1021086832201>
- Guidetti R, Altiero T, Rebecchi L (2011) On dormancy strategies in tardigrades. *J Insect Physiol* 57:567–576. <https://doi.org/10.1016/j.jinsphys.2011.03.003>
- Hairton NG (1996) Zooplankton egg banks as biotic reservoirs in changing environments. *Limnol Oceanogr* 41:1087–1092. <https://doi.org/10.4319/lo.1996.41.5.1087>
- Hairton NG, Cáceres CE (1996) Distribution of crustacean diapause: micro- and macroevolutionary pattern and process. *Hydrobiologia* 320:27–44. <https://doi.org/10.1007/BF00016802>

- Hartig F (2024) DHARMA: Residual diagnostics for hierarchical (Multi-Level / Mixed) regression models. R package version 0.4.7. <https://CRAN.R-project.org/package=DHARMA>
- Hoffmann PH, Adolfo A, Piu AG, Vendramin D, Martins L, Weber V, Maltchik L, Stenert C (2023) Invertebrate richness and hatching decrease with sediment depth in Neotropical intermittent ponds. *Wetlands* 43:24. <https://doi.org/10.1007/s13157-023-01675-6>
- Jocque M, Vanschoenwinkel B, Brendonck L (2010) Anostracan monopolisation of early successional phases in temporary waters? *Fundam Appl Limnol* 176:127–132. <https://doi.org/10.1127/1863-9135/2010/0176-0127>
- Koste W (1978) Rotatoria. Gebrüder Borntraeger, Stuttgart
- Le S, Josse J, Huisson F (2008) FactoMineR: an R package for multi-variate analysis. *J Stat Softw* 25:1–18. <https://doi.org/10.18637/jss.v025.i01>
- Lopes PM, Bozelli R, Bini LM, Santangelo JM, Declercq SAJ (2016) Contributions of airborne dispersal and dormant propagule recruitment to the assembly of rotifer and crustacean zooplankton communities in temporary ponds. *Freshw Biol* 61:658–669. <https://doi.org/10.1111/fwb.12735>
- Martinez-Ruiz C, Garcia-Roger EM (2015) Being first increases the probability of long diapause in rotifer resting eggs. *Hydrobiologia* 745:111–121. <https://doi.org/10.1007/s10750-014-2098-8>
- Mitsch W, Gosselink J (2015) *Wetlands*, 5th edn. John Wiley & Sons, Inc, Hoboken
- Nielsen DL, Smith FJ, Hillman TJ, Shiel RJ (2000) Impact of water regime and fish predation on zooplankton resting egg production and emergence. *J Plankton Res* 22:433–446. <https://doi.org/10.1093/plankt/22.3.433>
- Nielsen DL, Podnar K, Watts RJ, Wilson AL (2013) Empirical evidence linking increased hydrologic stability with decreased biotic diversity within wetlands. *Hydrobiologia* 708:81–96. <https://doi.org/10.1007/s10750-011-0989-5>
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, Mcglinn D, Minchin PR, O'Hara RB (2024) *Vegan: community ecology package* (ver. 2.6-6)
- Panarelli EA, Casanova S, Henry (2008) The role of resting eggs in the recovery of zooplankton community in a marginal lake of the Paranaapanema river (São paulo, Brazil), after a long drought period. *Limnologia* 20:75–90
- Penatti NC, Almeida TIRD (2012) Subdivision of pantanal quarternary wetlands: MODIS NDVI time-series in the indirect detection of sediments granulometry. *Int Arch Photogramm Remote Sens Spat Inf Sci XXXIX-B8*:311–316
- Pinceel T, Buschke F, Geerts A, Vanoverbeke J, Brendonck L, Vanschoenwinkel B (2021) An empirical confirmation of diversified bet hedging as a survival strategy in unpredictably varying environments. *Ecology* 102:e03496. <https://doi.org/10.1002/ecy.3496>
- Pires MM, Vendramin D, Medeiros ESF, Stenert C, Batzer DP, Maltchik L (2023) Bet-hedgers commit to the hedge: zooplankton in ephemeral semiarid wetlands of tropical Brazil that widely spread risk. *Ecology* 104:e4014. <https://doi.org/10.1002/ecy.4014>
- Poinar GO Jr (2010) Nematoda and nematomorpha. In: Thorp JH, Covich AP (eds) *Ecology and classification of freshwater invertebrates of North America*, 3rd edn. Academic, San Diego, pp 237–276
- Portinho JL, Perbiche-Neves G (2025) Effects of long-term desiccation on zooplankton resting egg banks from tropical lake sediments. *Fresh Biol* 70:e70037. <https://doi.org/10.1111/fwb.70037>
- Portinho JL, Nielsen DL, Ning N, Paul W, Nogueira M (2017) Spatial variability of aquatic plant and microfaunal seed and egg bank communities within a forested floodplain system of a temperate Australian river. *Aquat Sci* 79:515–527. <https://doi.org/10.1007/s00027-016-0514-z>
- R Core Team (2024) *R: A Language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria
- Radzikowski J (2013) Resistance of dormant stages of planktonic invertebrates to adverse environmental conditions. *J Plankton Res* 35:707–723. <https://doi.org/10.1093/plankt/ftb032>
- Rambo B (2000) A Fisionomia do Rio Grande do sul: ensaio de monografia natural. Unisinos, São Leopoldo
- Rebecchi L (2013) Dry up and survive: the role of antioxidant defences in anhydrobiotic organisms. *J Limnol* 72:62–72. <https://doi.org/10.4081/jlimnol.2013.s1.e8>
- Rebecchi L, Altiero T, Guidetti R (2007) Anhydrobiosis: the extreme limit of desiccation tolerance. *Invertebrate Surviv J* 4:65–81
- Ricci C (2001) Dormancy patterns in rotifers. *Hydrobiologia* 446:1–11. <https://doi.org/10.1023/A:1017548418201>
- Santangelo JM (2009) Produção, Ecloração e implicações ecológicas e evolutivas Dos estágios Dormentes do zooplâncton. *Limnotemas. Sociedade Brasileira de Limnologia*, Rio de Janeiro
- Schröder T (2005) Diapause in monogonont rotifers. *Hydrobiologia* 546:291–306. <https://doi.org/10.1007/s10750-005-4235-x>
- Seeliger U (1998) O sistema Das Dunas Costeiras Frontais. In: Seeliger U, Odebrecht C, Castello JP (eds) *Os ecossistemas Costeiro e Marinho do extremo Sul do Brasil*. Ecoscientia, Rio Grande, pp 179–184
- Sousa FDR, Elmoo-Loureiro LMA (2019) Identification key for the Brazilian genera and species of aloninae (Crustacea, branchiopoda, anomopoda, Chydoridae). *Pap Avulsos Zool* 59:e20195924
- Stenert C, Ehler B, Ávila AC, Sousa FDR, Esquinatti FM, Batzer DP, Maltchik L (2016) Dormant propagule banks of aquatic invertebrates in ponds invaded by exotic pine species in Southern Brazil. *Mar Freshw Res* 68:954–963. <https://doi.org/10.1017/MF16067>
- Stenert C, Wüsth R, Pires MM, Freiry RF, Nielsen D, Maltchik L (2017) Composition of Cladoceran dormant stages in intermittent ponds with different hydroperiod lengths. *Ecol Res* 32:921–930. <https://doi.org/10.1007/s11284-017-1498-4>
- Stewart NA, Schriever TA (2023) Local environmental conditions influence species replacement in great lakes interdunal wetland macroinvertebrate communities. *Freshw Biol* 68:46–60. <https://doi.org/10.1111/fwb.14008>
- Tuytens K, Vanschoenwinkel B, Waterkeyn A, Brendonck L (2014) Predictions of climate change infer increased environmental harshness and altered connectivity in a cluster of temporary pools. *Freshw Biol* 59:955–968. <https://doi.org/10.1111/fwb.12319>
- Vandekerckhove J, Declercq S, Jeppesen E, Conde-Porcuna JM, Brendonck L, De Meester L (2005) Dormant propagule banks integrate spatio-temporal heterogeneity in Cladoceran communities. *Oecologia* 142:109–116. <https://doi.org/10.1007/s00442-005-0020-9>
- Vanoverbeke J, Meester LD (2009) Within season short-term hatching delays suggest risk-spreading behaviour in populations of the freshwater Cladoceran daphnia. *Ecoscience* 16:441–451. <https://doi.org/10.2980/16-4-3254>
- Vanschoenwinkel B, Gielen S, Seaman MT, Brendonck L (2008) Any way the wind blows – frequent wind dispersal drives species sorting in ephemeral aquatic habitats. *Oikos* 117:125–134
- Vargas AL, Santangelo JM, Bozelli RL (2019) Recovery from drought: viability and hatching patterns of hydrated and desiccated zooplankton resting eggs. *Int Rev Hydrobiol* 104:26–33. <https://doi.org/10.1002/iroh.201801977>
- Vargas AL, Brazil T, Santangelo JM, Bozelli RL (2024) Long-term droughts change the hatching patterns of zooplankton resting eggs from permanent and temporary lakes. *Freshw Biol* 69:635–644. <https://doi.org/10.1111/fwb.14234>
- Vendramin D, Pires MM, Freiry RF, Schneider AEB, Martins L, Medeiros ESF, Rocha O, Stenert C, Maltchik L (2022) Hatching

- dynamics of invertebrate dormant stages in temporary ponds are influenced by multiple hydrations. *Freshw Sci* 41:143–152. <https://doi.org/10.1086/719129>
- Vendramin D, Pires MM, Medeiros ESF, Stenert C, Maltchik L (2023) Life finds a way: hatching dynamics of zooplankton dormant stages in intermittent wetlands from the Brazilian tropical semi-arid. *J Arid Environ* 212:104949. <https://doi.org/10.1016/j.jarideenv.2023.104949>
- Weber V, Alonso F, Godoy RS, Lanes LEK, Pires MM, Stenert C, Gava A, Maltchik L (2025a) Hitting and unmissing the pause button: variable hatching patterns of annual killifish embryos over a wetland wet-dry cycle. *Ecol Freshw Fish* 34:e12816. <https://doi.org/10.1111/eff.12816>
- Weber V, Alonso F, Godoy RS, Lanes LEK, Pires MM, Gava A, Stenert C, Maltchik L (2025b) Evolved bet-hedging through maternal effects: developmental trajectory variation in annual killifish across a wet-dry cycle. *Hydrobiologia*. <https://doi.org/10.1007/s10750-025-05962-7>
- Wickham H (2016) *ggplot2: elegant graphics for data analysis*. Springer, New York
- Williams DD (2006) *The biology of temporary waters*. Oxford University Press, New York
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